THE STRUCTURE AND RELATIONSHIPS OF THE JURASSIC FISH *ICHTHYOKENTEMA PURBECKENSIS*

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SYNOPSIS

Ichthyokentema purbeckensis (Davies), a halecostome from beds of marine or hypersaline origin in the lower half of the Purbeck, is described in detail. The species differs from known members of the Pholidophoridae in a number of characters, especially in the structure of the snout, and a new family Ichthyokentemidae is made to contain it. Variations in the structure of the snout in halecostomes are shown to separate the group into at least two lines which may be only distantly related. The origin of the halecostomes is to be found near the Parasemionotidae, but it is considered that the parasemionotids are unlikely to have been directly ancestral to the group because of the structure of their neurocrania. The evolution of the fossa bridgei is discussed, and it is concluded that the post-temporal fossa of holosteans and teleosts is not homologous with the fossa bridgei, but is a new structure which has replaced the latter.

I. INTRODUCTION

IN 1958 and 1959 the authors and Dr. B. G. Gardiner collected a large number of disarticulated fish bones from the Lower Purbeck Broken Beds near Lulworth Cove, Dorset. The bulk of this material has proved to belong to *Ichthyokentema purbeckensis*

(Davies), a species previously known by about a dozen complete but crushed specimens. The new material has enabled us to produce an almost complete description of the species. *Ichthyokentema* is found to differ in some important respects from *Pholidophorus*, to which it was thought to be closely related, and these differences have led us to form some new opinions on the origin and evolution of the halecostomes.

The classification used is that of Arambourg & Bertin (1958), in which the " holosteans " are divided into two super-orders, Holostei and Halecostomi, the latter being further divided into the orders Pholidophoriformes, Leptolepiformes and Aspidorhynchiformes.

II. MATERIAL AND CONDITIONS OF DEPOSITION

The material on which this account is based consists of the British Museum (Natural History) collection of *Ichthyokentema purbeckensis* together with the new material of this species collected in Dorset and since added to the British Museum collection.

The new material consists of several hundred specimens collected from the Broken Beds near Lulworth Cove. The Broken Beds contain up to 15 ft. of fissile, sandy limestone which have become shattered and deformed into a coarse breccia. The processes responsible for this deformation are discussed by Arkell (1938) and Hollingworth (1938). The conclusion reached by these authors is that the Broken Beds result from Tertiary tectonic action on beds previously weakened by the solution of gypsum. This has been confirmed by the proving of gypsum *in situ* at the horizon of the Broken Beds in boreholes below the Weald.

At Lulworth there is a 6-in. band of yellow-brown, sandy limestone, darker in colour than the surrounding purer limestone, lying about 6 ft. 3 in. below the top of the Broken Beds. Eight inches below this band there is a similar band, 3 to 5 in. thick. The fishes were found in the 3 ft. 6 in. of limestone directly below this band. The specimens were collected from a single large block, about 10 ft. long and 4 ft. thick, lying immediately above the " fossil forest " where it is exposed in the cliff a quarter of a mile east of the mouth of Lulworth Cove. The bones were distributed throughout 3 ft. 6 in. of sediment, and were common everywhere, though more abundant in and near the clay partings which occur irregularly in the rock. The fish remains are all disarticulated, only the neurocrania, mandibles and pectoral girdles being preserved reasonably intact. Though the bones lie scattered throughout the rock, they are perfectly preserved, and show no signs of rolling or abrasion. There are some signs that the bones have been water sorted, for while no specimen shows scattered remains of a single skeleton, it is common to find two or three neurocrania lying close together with no other bones in their vicinity. The vast majority of the bones are of *Ichthyokentema purbeckensis* : we have parts of at least 50 neurocrania of this species. A few fragments of other fishes are present, including a maxilla, a preoperculum, a hyomandibular, a dentary, an angular, vertebrae and scales of a leptolepid, scales and teeth of a holostean and some undetermined teeth. Associated with the fishes are fragmentary plant remains and abundant ostracods of the two species " *Cypris* " *purbeckensis* Forbes and *Fabanella bononiensis* (Jones) (= *Candona bononiensis*), with the former more abundant.

The British Museum collection contains eleven specimens of *Ichthyokentema purbeckensis* including the holotype and three specimens in counterpart. All the specimens are complete fishes, not fragments like the Lulworth material, and all are from the Purbeck beds, though the precise horizon and locality are recorded for very few. The holotype, P. 6171, is from the Lower Purbeck of the Isle of Portland, and two other specimens, 40635 and P. 12515 are from the same horizon and locality. P. 7640 is from the Lower Purbeck " White Lias " of the Teffont Lime Kiln quarry, Teffont Evias, Wilts. There are three bands of " White Lias "—a hard, white marl—at Teffont, all in the Lower Purbeck (Woodward, 1895 : 271), and the exact horizon of the specimen is therefore unknown, but the British Museum collection includes specimens of *Leptolepis brodiei, Pleuropholis formosa* and *Ceramurus macrocephalus* from the same rock at this locality, and the holotype of *P. formosa*, P. 10986, is labelled as being from the second band of " Lias ", which lies near the base of the Lower Purbeck, at the same horizon as the Broken Beds. The only other fossils contained in this " White Lias " matrix are minute bodies which Dr. F. W. Anderson suggests are algal fragments. P. 1074, the holotype of *Pholidophorus brevis* Davies (shown below to be a synonym of *I. purbeckensis*) and P. 1073/3607, a specimen in counterpart previously referred to *P. brevis*, are both labelled as being from the Upper Purbeck of Upway, near Weymouth, but Strahan (1898 : 108) describes Upway as showing Lower Purbeck beds only, and the matrix of the specimens appears identical with that in the Broken Beds, suggesting that the specimens are in fact from the Lower Purbeck. This has been confirmed by Dr. F. W. Anderson, who has identified the typical Lower Purbeck ostracods " *Cypris* " *purbeckensis* and *Fabanella bononiensis* in the matrix. Of the remaining five specimens, P. 8378 and P. 8379 are from the Purbeckian of the Isle of Portland, P. 12347 is from the Purbeckian of Swanage, and P. 7640 and P. 7807 are of unknown provenance. With the exception of the specimen from Teffont and P. 12347, all the specimens are in matrices which appear identical with the Broken Beds, with plant fragments and " *Cypris* " *purbeckensis*. P. 12347 is in a crystalline, shelly limestone : the shells are of bivalves, but are too poorly preserved for identification. In this matrix Dr. Anderson has identified one specimen of *Cypridea granulosa* (Sowerby), an ostracod characteristic of brackish water facies in the lower part of the Middle Purbeck. Dr. Anderson places the specimen at a horizon about 12 ft. below the Cinder bed. The known range of *I. purbeckensis* is thus from the base of the Lower Purbeck to the lower part of the Middle Purbeck.

The ostracods " *Cypris* " *purbeckensis* Forbes and *Fabanella bononiensis* (Jones), previously thought to be freshwater forms (Arkell, 1933 : 534), are now known to be typical of a marine or hypersaline facies (Anderson, 1958 : 128). The Broken Beds, containing gypsum and a very limited fauna of ostracods and fish, with no molluscs, obviously represent a hypersaline facies, and must have been laid down in a partially or completely enclosed body of salt water in which the salt concentration was raised periodically or maintained at a high level by evaporation. All but two of the known specimens of *I. purbeckensis* come from this type of deposit, suggesting that the species was marine, though the possibility of the fish having been washed into the body of salt water with an influx of fresh water is not completely excluded. The other two matrices from which the fish is known do not give definite confirmation of a marine habitat ; the " White Lias ", with no other fossils except algal fragments, is obviously representative of a specialized habitat, neither purely freshwater nor marine, while the shelly matrix of P. 12347 with a single specimen of the brackish water ostracod *Cypridea granulosa* (Sowerby) indicates a brackish water deposit. The absence of the species from any of the freshwater deposits of the Purbeck tends to confirm that the habitat was marine. The balance of the evidence indicates that *I. purbeckensis* was a marine fish, possibly adapted to hypersaline conditions. The association of *Leptolepis brodiei*, *Pleuropholis formosa* and *Ceramurus macrocephalus* with *Ichthyokentema purbeckensis* in the " White Lias " at Teffont suggests that these three species were also marine.

III. METHODS

The new material from Lulworth was prepared mainly by dissolving the matrix with dilute acetic acid. Attempts were made both with the British Museum material and the new material to embed specimens in resin and remove the matrix with acid, but the rock proved too marly for this method to give good results. The scales removed from the Lulworth matrix were too friable for satisfactory sectioning, but excellent preparations were made by washing the dried scales in xylene and mounting in Naphrax : when examined in transmitted light these preparations show the structure of the scales very clearly (Pl. 2, fig. 6). Text-figures 1, 6 and 7 are based on photographs of a plasticine model on to which enlarged outlines of the individual bones were fitted. All specimens are referred to by their registered numbers in the British Museum (Natural History). Numbers in the series P. 44923–79 and P. 45020–39 refer to the new material from Lulworth, other numbers refer to older specimens.

IV. DESCRIPTION

Super-Order Halecostomi. For diagnosis see Arambourg & Bertin, 1958 : 2195

Order Pholidophoriformes

For diagnosis see Berg, 1940: 214 but add " maxilla with one or two supramaxillae " and delete " mandible . . . . without coronoids ".

Family Ichthyokentemidae nov.

Diagnosis. Small, fusiform Pholidophoriformes ; the bones of the head and scales ganoine covered but not strongly ornamented ; a toothed rostral separating the premaxillae ; nasals broadly in contact in the mid-line ; supraorbital sensory canal ending in the parietal and having no anastomosis with the infraorbital canal, anterior and middle pit-lines on the parietal, the latter extending on to the dermopterotic ; neurocranium ossified in separate bones, but some fusion in the otic region in the adult, ethmoid region a single ossification, interorbital septum poorly ossified, no aortic groove or canal below the occipital condyle, lateral wall of jugular canal very weakly ossified, basisphenoid pedicel with a pair of canals for the internal carotids, vomer unpaired ; dermosphenotic elongated dorso-ventrally, second infraorbital below the dermosphenotic enlarged and bearing horizontal and vertical pit-lines; a single suborbital; four supraorbitals; suspensorium slightly inclined forwards; a single supramaxilla; mandible with dentary, articular, a fully ossified Meckel's cartilage and a single coronoid, oral pit-line present on articular; teeth borne on rostral, premaxilla, maxilla, vomer, parasphenoid, endopterygoid, dentary and coronoid; a single gular; preopercular not expanded at the angle, suture between opercular and subopercular almost horizontal; vertebrae with annular centra, notochord almost unconstricted, neural and haemal arches fused with centra, ribs articulating with short transverse processes, no epipleurals or epineurals; suprascapular large, endoskeletal pectoral girdle ossified in a single piece, mesocoracoid arch present; large fulcra present on all fins; scales rhomboid, with bone cells and canals of Williamson, hind edge not pectinated, the single lateral line passing through a row of deepened scales on the flank.

Genus *ICHTHYOKENTEMA* A. S. Woodward, 1941 : 90.

DIAGNOSIS. As for family (only genus).

TYPE SPECIES. ***Pholidophorus purbeckensis*** Davies.

Ichthyokentema purbeckensis (Davies)

(Pls. 1–4; Text-figs. 1–14)

1887. *Pholidophorus purbeckensis* Davies, p. 337, pl. 10, figs. 2–4.
1887. *Pholidophorus brevis* Davies, p. 338, pl. 10, fig. 1.
1888. *Pholidophorus purbeckensis* Davies : Davies *in* Damon, p. xix, pl. 19, fig. 1.
1895. *Pholidophorus purbeckensis* Davies : A. S. Woodward, p. 460.
1919. *Pholidophorus purbeckensis* Davies : A. S. Woodward, p. 108, pl. 22, figs. 1–3.
1919. *Pholidophorus brevis* Davies : A. S. Woodward, p. 110, pl. 22, figs. 4, 5.
1941. *Ichthyokentema purbeckensis* (Davies) A. S. Woodward, p. 90.
1941. *Ichthyokentema brevis* (Davies) A. S. Woodward, p. 90.

A. S. Woodward (1895 : 460) considered *Pholidophorus brevis* Davies to be a synonym of *P. purbeckensis*, but later (1919 : 110) he reinstated the species, finding it to be " shorter and stouter " than *P. purbeckensis* and to come from the Upper Purbeck, while *P. purbeckensis* ranged from the Lower to Middle Purbeck. It is shown above, however, that the specimens referred to *P. brevis* are in fact from the Lower Purbeck. We have been able to find no characters by which these specimens may be differentiated from *I. purbeckensis*, and are of the opinion that *I. brevis* is a synonym of *I. purbeckensis*.

EMENDED DIAGNOSIS. A species of *Ichthyokentema* reaching about 7 cm. in standard length, length of head slightly greater than maximum depth of trunk and equal to about three-tenths of the standard length; fin formula: P.11+; V.5+; D.9; A.6–7; C.19; ten or eleven scales in each transverse series on the trunk, about thirty-five scales along the lateral line, lateral line scales up to four times as deep as long.

HOLOTYPE. British Museum (Natural History) No. P. 6171.

(a) *Measurements and Proportions*

Measurements of the more complete specimens are given in Table I and a photograph of P. 8378 is shown in Pl. 1, fig. 1. The specimens are small, most of them having a total length of between 6 and 8 cm. Roughly 30 per cent of the total length is occupied by the head and the maximum depth of the trunk is equal to nearly the same fraction of the total length. The fins are of moderate size. The pelvic fins lie a little nearer to the tip of the snout than to the fork of the caudal fin. The dorsal and anal fins are triangular and of approximately equal size ; the dorsal commences a short distance behind the level of the pelvics and the anal a little further back still. The caudal fin, which is moderately deeply forked, is of hemiheterocercal type.

While it is impossible to obtain measurements of the individuals from which the fragmentary material from Lulworth is derived, the fragments themselves are similar in size to the corresponding parts of the more complete specimens.

Table I

(All measurements in mm.)

Specimen No.	Tip of snout to fork of caudal fin	Tip of snout to origin of anal fin	Length of skull (including operculum)	Maximum depth of trunk
P. 7640	c 44	27·5	12	11·5
P. 8378	64	40	c 18·5	17
P. 12515	67	42	19·5	17
P. 8379	c 68	c 45	c 19·5	17
P. 7807	71	47	c 20·5	18
40635a	76	53	—	20·5
P. 3607, P. 1073	—	52	23	23·5
P. 1074	64	43	18	23
P. 6171	c 68	c 43	—	20

(b) *Neurocranium and Skull Roof*

The skull roof is shown in Text-fig. 1 and Pl. 2, fig. 3, and lateral, ventral and posterior views of the reconstructed neurocranium are shown in Text-figs. 2 to 4. Pl. 3, figs. 7, 8 show stereoscopic pairs of the neurocranium in ventral view and the cranial cavity in dorsal view.

The neurocranium is long, and only about two-thirds as deep as it is broad. The orbit is large, and the interorbital septum is very incompletely ossified. The neurocranium is well ossified, with few cartilagenous interspaces in its walls. The sutures between the cartilage bones are often indistinguishable on the external surface of the neurocranium, but they can usually be recognized on the internal surface of the bones.

The dermal roof of the skull is flat, and gently rounded in the transverse plane. The parietal (pa.) is about as large as it is in *Pholidophorus similis* (Saint-Seine, 1949 : 216) and is a rectangular bone, meeting its fellow in the mid-line, the frontal anteriorly, the dermopterotic laterally, and overlying the epiotic and supraoccipital. The parietal bears the anterior pit-line, the medial part of the middle pit-line, and, in most specimens, the terminal part of the supraorbital sensory canal. The bone is ornamented with a few weak ridges radiating from its postero-medial corner.

The frontal (fr.) is the usual very large bone, meeting its fellow in the mid-line and the parietal and dermopterotic posteriorly. Above the orbit the lateral edge of the frontal is perfectly smooth, and shows no signs of the articulation of the supraorbitals. The frontal is ornamented with weak ridges which radiate from its centre, and are shorter and more irregular on the posterior part of the bone. Anteriorly, the frontal tapers and ends over the ethmoid.

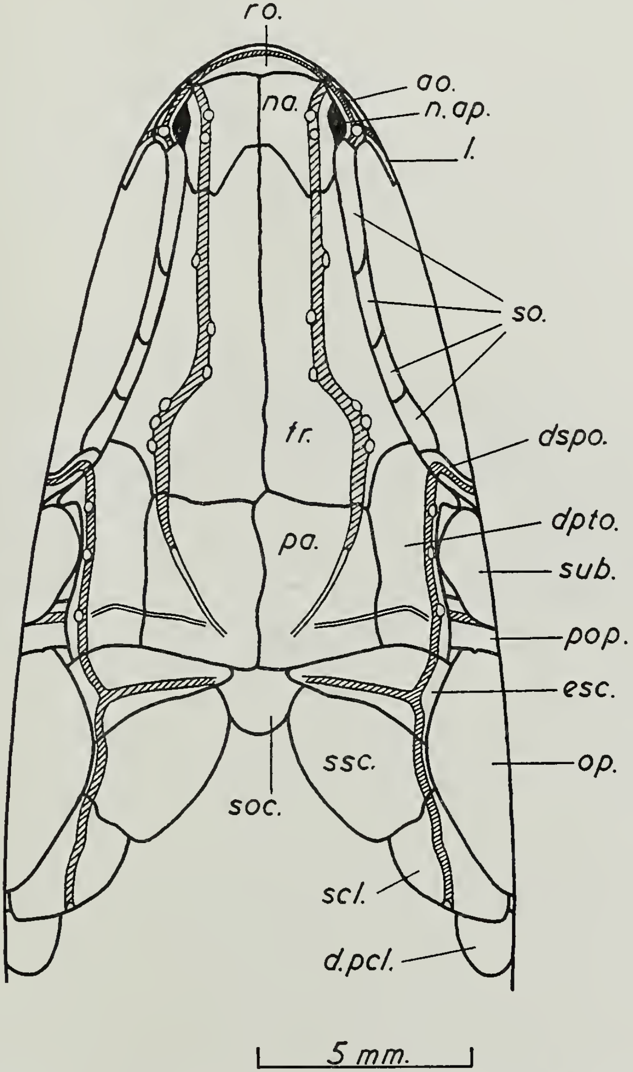

FIG. 1. *Ichthyokentema purbeckensis.* Reconstruction of skull and pectoral girdle in dorsal view. For explanation of lettering see p. 43.

The dermopterotic (dpto.) is a stout, rectangular bone which forms the roof of the post-temporal fossa, meeting the parietal medially and the autopterotic ventro-laterally. At the posterior edge of the orbit the dermopterotic bears a process pointing ventro-laterally: the dermosphenotic articulates with the anterior face of this process, and its posterior face forms the anterior wall of the dilatator fossa. The dermopterotic is ornamented with short, irregular ridges radiating from the middle of its lateral edge. The main cephalic sensory canal entered the dermopterotic from the extrascapular through a large pore in the posterior edge of the bone, above the lateral part of the post-temporal fossa. The preopercular sensory canal passed ventrally to the preopercular through a large pore at the posterior end of the lateral edge of the dermopterotic. Passing forwards through the dermopterotic, the canal gave off two branches through pores in the dorso-lateral edge of the bone, and then passed into the dermosphenotic through a pore in the anterior edge of the postorbital process. The supraorbital sensory canal did not anastomose with the infraorbital sensory canal. In some specimens the supraorbital canal ends posteriorly at the posterior edge of the frontal, but in most specimens it passes into the parietal and may extend for half the length of this bone (P. 44923). In the frontal, the supraorbital canal ran from end to end of the bone in a tube which roughly follows the contour of the edge of the bone. The canal gave off between five and seven branches through pores in the frontal. The number and position of these pores varies from specimen to specimen, and from side to side of the same specimen, but there is usually a cluster of three pores above the posterior edge of the orbit. The canal passed forwards to the nasal from the anterior end of the frontal. The anterior pit-line runs back postero-medially across the parietal from the terminal pore of the supraorbital canal almost to the posterior edge of the bone. The middle pit-line runs transversely

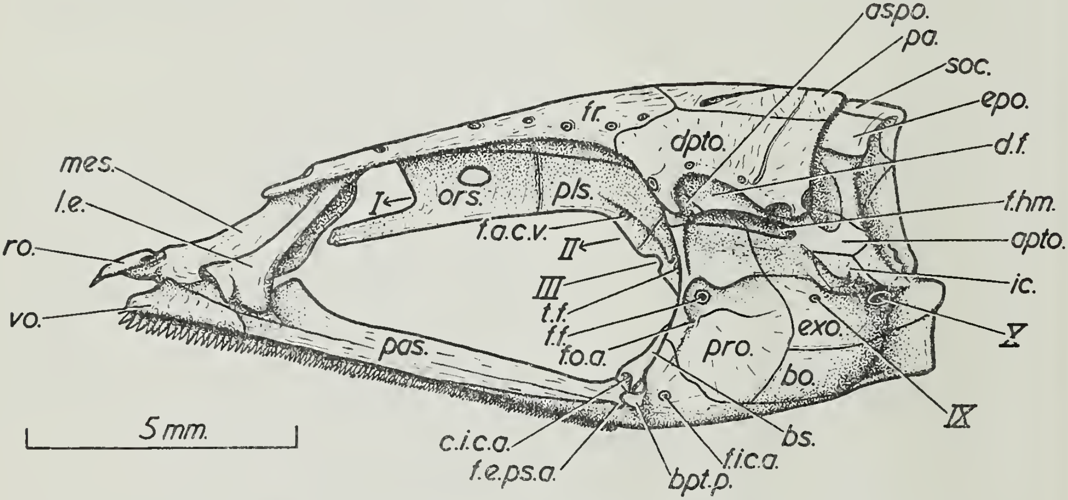

FIG. 2. *Ichthyokentema purbeckensis*. Reconstruction of neurocranium in lateral view. For explanation of lettering see p. 43.

from the region of the hind end of the anterior pit-line, and extends almost to the lateral edge of the dermopterotic, where it ends over the main cephalic canal.

The nasal (na., Pl. 2, fig. 5) (P. 8379 ; P. 7640 ; P. 44924–25) is a roughly triangular bone which carried the terminal part of the supraorbital sensory canal in a tube near its lateral edge. The nasals met in the mid-line through the greater part of their length. A shallow notch in the lateral edge of each nasal formed the dorsal margin of a narial aperture (n.ap.) : both nostrils may have opened through this single aperture, but it is possible that there was an anterior nostril between the antero-lateral edge of the nasal, the rostral and the antorbital. The pointed posterior end of the nasal articulated with the frontal, and received the sensory canal from the latter. The sensory canal gave off two branches through pores in the nasal, and passed forwards from the anterior end of the bone to anastomose with the ethmoid commissure at the junction between the antorbital and the rostral. Medial to the tube which contained the sensory canal the nasal bears a few ornamental bosses.

The ethmoid region is well ossified superficially, but in life the bone was a thin sheet over the surface of a block of cartilage which was exposed ventrally. There is no visible suture separating the mesethmoid and lateral ethmoid. The mesethmoid (mes.) is represented by a median ridge running forwards beyond the frontals, and widening anteriorly where the rostral articulates with its dorsal surface. The lateral ethmoid (l.e.) is represented by a strong wing extending antero-ventrally beneath the frontal. The lachrymal articulated with the thickened ventro-lateral edge of this wing, and the palatine articulated with the cartilage capping the ventral edge of the wing. Between the mesethmoid and lateral ethmoid regions there is a large depression, open dorsally, which housed the olfactory organ.

The rostral (ro., Pl. 2, figs. 4, 5) (P. 8379 ; P. 44926–27) is a median, triangular bone overlying the tip of the mesethmoid and projecting beyond the latter. The anterior edge of the bone bears a single row of about a dozen small teeth. There is a projection on the lateral edge of the bone with which the premaxilla articulated. The rostral commissure, received laterally from the antorbital, ran in a closed tube across the posterior part of the bone.

The vomer (vo.) (P. 44927–28) is thick and broad, and bears about 50 stout, slightly curved teeth on its ventral face. On the dorsal surface of the bone there is a pair of short wings which meet the mesethmoid above. The head of the maxilla articulated with a facet at the base of the wing of the vomer, and the palatine articulated with the lateral edge of the bone. The vomer is a median bone and shows no sign of a paired origin : it thus resembles the vomer of teleosts. The vomer is not known in any other halecostome, nor is it known in parasemionotids.

The parasphenoid (pas.) (P. 44927 ; P. 44929–30) is long and stout. It is narrow below the orbit, but widens anteriorly, where it ends in a groove on the dorsal surface of the vomer. The parasphenoid bears an elongated patch of teeth which extends from its anterior end to the level of the basipterygoid process. The teeth grow smaller posteriorly as the patch of teeth narrows. Below the orbit the bone bears a median crest which gave insertion to the ventral edge of the membranous interorbital septum. This crest ends posteriorly at the level of the pedicel of the basisphenoid, which articulated with its hind edge. Behind this crest there is in some specimens (e.g. P. 44931–32) a wide bucco-hypophysial canal (b.h.c.) which passes obliquely antero-ventrally through the bone, but this canal is not a constant feature. An open bucco-hypophysial canal is a primitive feature which has so far been observed among actinopterygians only in a few chondrosteans and in the teleost *Elops* (Olsson, 1958).

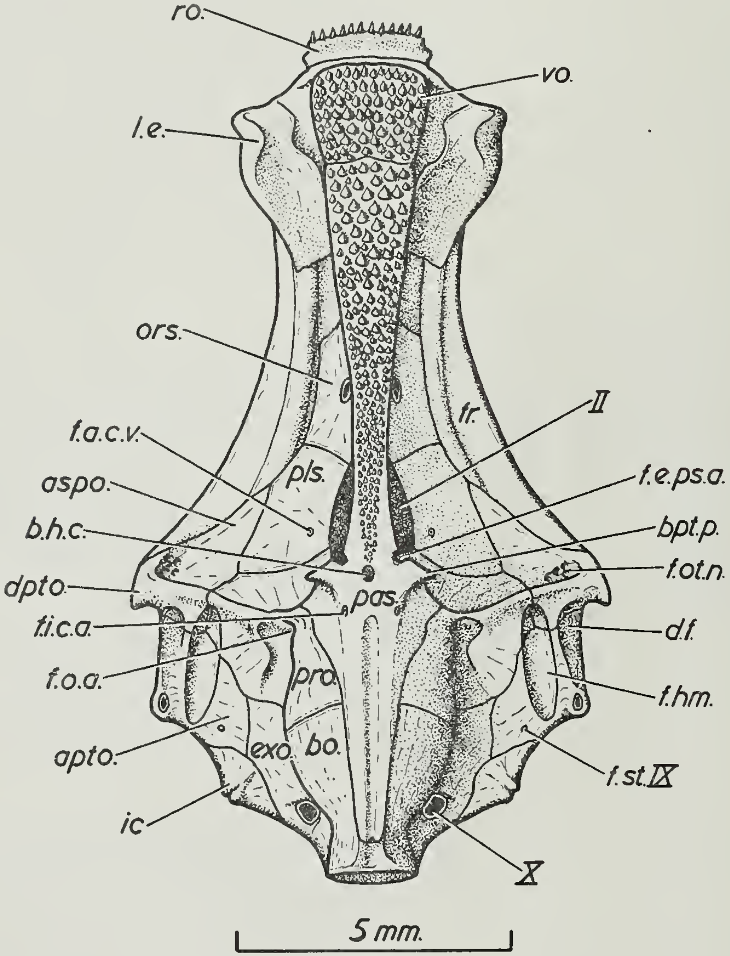

Fig. 3. *Ichthyokentema purbeckensis.* Reconstruction of neurocranium in ventral view. For explanation of lettering see p. 43.

At the hind edge of the orbit the parasphenoid bears a short basipterygoid process (bpt.p.) which is shorter than those of both *Leptolepis* and *Pholidophorus*. The ascending process of the parasphenoid, behind the basipterygoid process, is short and delicate. The foramen of the internal carotid artery (f.i.c.a.) lies in the centre of the ascending process. A notch (f.e.ps.a.) at the base of the anterior edge of the basipterygoid process marks the passage of the efferent pseudobranchial artery (in some specimens, e.g. left side of P. 44933, this notch is enclosed within the bone as a foramen). The posterior part of the parasphenoid meets the prootic and basioccipital: it closes the myodome ventrally and ends just in front of the occipital condyle.

On the internal face of the ascending process of the parasphenoid, antero-dorsal to the internal carotid foramen, there is a bar of bone passing medially to meet the tip of the basisphenoid (Text-fig. 5; P. 44930–33): the internal carotid and the palatine nerve passed forwards below this bar.

The basioccipital (bo.) (P. 44927; P. 44934–35) forms the major part of the occipital condyle. The notochord pit, in the centre of the basioccipital condyle, is very long, and extends to the anterior edge of the basioccipital. This is a primitive feature recalling the chondrosteans. The anterior part of the basioccipital consists of a lateral wall which bulges out to meet the prootic anteriorly and the exoccipital above, and a broad median crest which tapers anteriorly and meets the similar crest formed by the prootics. The lateral wall forms the wall of the otolith chamber while the median crest separates the otolith chambers and encloses the notochord pit. On the ventral surface of the basioccipital there is a median groove which is bridged by the parasphenoid, but there is no groove or canal for the dorsal aorta as there is in *Pholidophorus bechei* (Rayner, 1948 : 322) and *Leptolepis coryphaenoides* (Rayner, 1937 : 57).

Each exoccipital (exo.) forms a small triangular exoccipital condyle applied to the dorso-lateral edge of the basioccipital condyle. The triangular foramen magnum (f.m.) is enclosed between the exoccipitals above the occipital condyle. Lateral to the foramen magnum, the exoccipital bears several small, projecting crests (Text-fig. 4). These crests may mark the insertion of the anterior myocommata on the skull, or they may be the sites of insertion of ligaments binding the first neural arch to the skull. The occipital nerves emerged through one or two small foramina between the crests on the exoccipital (f.o.n.) (P. 44936–37). On the posterior face of the neurocranium the exoccipital touches the supraoccipital dorsally, and meets the epiotic dorso-laterally and the autopterotic laterally, the suture with the latter being partially overlain by the intercalar. On the lateral face of the neurocranium the exoccipital meets the prootic and basioccipital, forming with these bones the wall of the otolith chamber, and meets the autopterotic above, though the suture with the latter bone is never clear, and the bones were evidently more or less fused. The large vagus foramen (X) opens postero-laterally at the posterior edge of the lateral face of the exoccipital. The glossopharyngeal foramen (IX) lies near the anterior edge of the lateral face of the bone. Internally, the exoccipitals form the posterior part of the floor of the cranial cavity, where they overlie the median crest of the basioccipital and form the posterior margin of the fenestra between the otolith chamber and the cranial cavity (P. 44934).

The autopterotic (apto.) forms the floor of the posterior part of the post-temporal fossa, and meets the autosphenotic anteriorly, the epiotic medially, the exoccipital postero-ventrally and the prootic antero-ventrally. Laterally the autopterotic meets the dermopterotic, which roofs the post-temporal fossa. The autopterotic appears to be fused with the dermopterotic anteriorly, above the dilatator fossa. In the anterior part of the floor of the post-temporal fossa there was an area of cartilage (c.t.f., Pl. 3, fig. 8) which separated the autopterotic from the autosphenotic. The posterior three-quarters of the elongated facet for the hyomandibular (f.hm.) is borne on the ventral face of the autopterotic, and above this facet the shallow posterior part of the dilatator fossa (d.f.) is excavated in the lateral edge of the bone. Medial to the hind end of the hyomandibular facet, the autopterotic is perforated by a small foramen (f.st.IX) which transmitted the supratemporal branch of the glossopharyngeal nerve upwards across the post-temporal fossa to the sensory canal on the skull roof (P. 44934). Internally, the autopterotic enclosed the external semicircular canal and the ventral part of the posterior semicircular canal (P. 44934) The intercalar (ic.) (P. 44938) is the usual small, superficial bone, plastered on the surface of the exoccipital and autopterotic. Two knobs with a notch between them mark the insertion on the bone of the ligament from the ventral limb of the suprascapular.

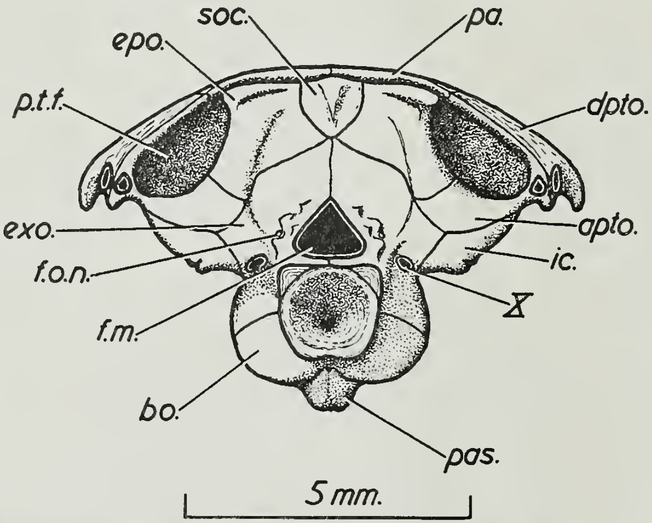

Fig. 4. *Ichthyokentema purbeckensis*. Reconstruction of neurocranium in posterior view. For explanation of lettering see p. 43.

The epiotic (epo.) forms the postero-dorsal shoulder of the neurocranium, as usual. The anterior part of its dorsal surface is overlain by the parietal and dermopterotic, and the extrascapular and suprascapular articulated with its exposed dorsal surface. Laterally, the epiotic forms the medial wall of the post-temporal fossa, meeting the autopterotic below. The epiotics are separated by the supraoccipital, and they meet the exoccipitals on the posterior face of the neurocranium. The angle between the lateral and posterior faces of the epiotic forms a thickened buttress within which the dorsal part of the posterior semicircular canal was enclosed (p.s.c., Pl. 3, fig. 8) (P. 44934.)

The supraoccipital (soc.) is moderately large, being overlain by the parietals anteriorly, and extending down the posterior face of the neurocranium to touch the exoccipitals. There is a small, knob-like crest on the posterior face of the bone. It is possible that the supraoccipital was exposed on the skull roof between the medial edges of the extra- and supra-scapulars, but this is not certain.

The autosphenotic (aspo.) is a rather small bone, underlying the frontal and dermopterotic, and meeting the prootic below and autopterotic behind. Anteriorly the bone tapers to a point between the frontal and the pleurosphenoid. The broad upper part of the ridge marking the hind edge of the orbit is formed by the autosphenotic, and behind this ridge the bone forms the antero-dorsal corner of the hyomandibular facet. Above the hyomandibular facet the autosphenotic bears the anterior part of the dilatator fossa (d.f.), an excavation which housed the dilatator muscle of the operculum. In the dorso-lateral corner of the orbit there are several small pits (f.ot.n.) in the autophenotic which mark the passage of the otic branch of the facial nerve.

The post-temporal fossa (p.t.f., Text-fig. 4) is completely roofed by the dermopterotic. The fossa has a large, oval posterior opening, and extends forwards, tapering as it does so, as far as the hind edge of the orbit (P. 44934), where it ends between the autosphenotic and dermopterotic.

The prootic (pro.) (P. 44934 ; P. 44939–40), as usual, is the most complex bone in the neurocranium. The ventral part of the bone consists of an outer lamella which bulges out to form the anterior part of the wall of the otolith chamber, and an inner lamella which separates the myodome from the otolith chamber and meets its fellow above the myodome in the prootic bridge (pro.b., Text-fig. 5 ; Pl. 3, fig. 8). The inner and outer lamellae meet anteriorly in the posterior edge of the orbit. The dorsal part of the prootic consists of a lateral region which meets the autosphenotic and the autopterotic, and forms the antero-ventral corner of the hyomandibular facet, and an anterior region which forms the posterior wall of the orbit, meeting the pleurosphenoid above and being separated from its fellow by the wide median optic fenestra (II). Between the dorsal and ventral parts of the bone, lateral to the prootic bridge, the prootic contains the trigemino-facialis chamber. The chamber is divided by a wall of bone into an internal pars ganglionaris and an external pars jugularis, as it is in teleosts, *Leptolepis*, *Pholidophorus* and most fossil holosteans. The pars ganglionaris is a very shallow recess on the medial face of the prootic. The geniculate ganglion certainly lay within the pars ganglionaris, since the palatine nerve left the main trunk of the facial before the latter emerged from the facial foramen. The position of the Gasserian ganglion is not certain : it may have lain in the pars ganglionaris or it may have lain partially or completely outside the prootic, on the orbital surface of the bone. The pars jugularis is a longitudinal groove on the lateral face of the prootic. The lateral wall of the pars jugularis is very poorly ossified ; in some specimens (e.g. P. 44941–42 ; Text-figs. 2, 3, 5) there is a narrow bar of bone bridging the anterior end of the groove, but in others (e.g. P. 44934–39) there are two processes in this region which fail to meet each other. The ridge marking the upper edge of the pars jugularis is stronger than that marking the lower edge, and can be traced back on to the exoccipital.

The jugular vein ran in this groove, passing back from the orbit below the lateral wall of the groove where the latter is present. The course of the orbital artery, passing up from the internal carotid, is marked by a break in the ventral edge of the jugular groove (f.o.a., Text-figs. 2, 3) above the internal carotid foramen. The orbital artery passed forwards into the orbit with the jugular vein. Only one foramen leads from the pars ganglionaris into the pars jugularis : this is the facial foramen (f.f., Text-figs. 2, 5 ; Pl. 3, fig. 8) which, in about half the specimens, transmitted only the hyomandibular trunk of the facial nerve. Within the bone, there are two canals leaving the floor of the facial foramen. The larger of these passes antero-ventrally into the dorso-lateral corner of the myodome, and transmitted the palatine nerve (VII p., Text-fig. 5). The smaller canal passes postero-ventrally through the prootic in front of the otolith chamber. Though this second canal is a constant feature, it could not be traced to an external opening in any specimen, and it may have carried a blood vessel. The trigeminal foramen (t.f., Text-figs. 2, 3, 5 ; Pl. 3, fig. 8) opens on the orbital face of the prootic, and the trigeminal nerve did not enter the pars jugularis. On the medial face of the prootic, in the pars ganglionaris, the trigeminal foramen lies antero-dorsal to the facial foramen. In about half the specimens in which this region is visible there is a third foramen which lies immediately above the facial foramen (P. 44939) or is confluent with the latter (P. 44943–44 ; right side of P. 44940), and which opens on the orbital surface of the prootic just postero-dorsal to the trigeminal foramen (VII lat., Text-fig. 5). This foramen must have transmitted the lateralis branches of the facial nerve, the buccal, otic and superficial ophthalmic nerves. In other specimens (P. 44933–34 ; P. 44941 ;

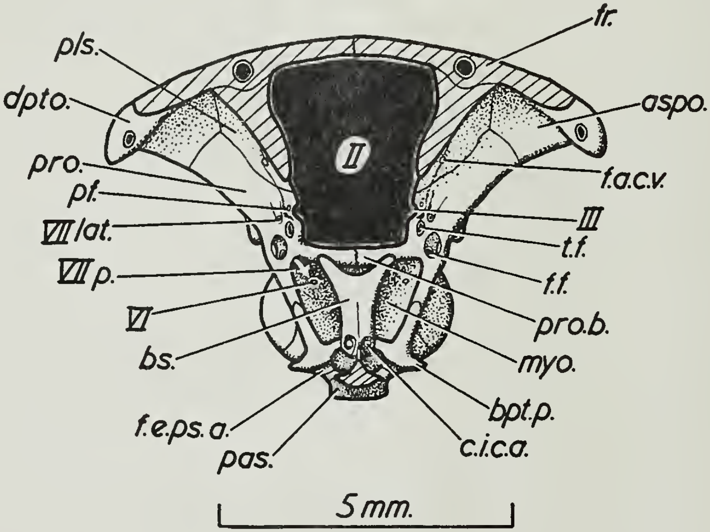

Fig. 5. *Ichthyokentema purbeckensis.* The reconstructed neurocranium cut through immediately anterior to the basisphenoid and viewed from the front. For explanation of lettering see p. 43.

left side of P. 44940) this foramen is absent, and the lateralis branches of the facial nerve passed through the facial foramen and forwards into the orbit with the jugular vein. In the orbital edge of the prootic, anterior to the trigeminal foramen, there is a notch (III) which marks the passage of the oculomotor nerve. Between the trigeminal foramen and the oculomotor notch there is a knob from which a ridge passes dorsally, widening as it does so. The superficial ophthalmic nerves and the otic nerve passed upwards behind this ridge. In some specimens the knob in front of the trigeminal foramen is perforated by a small canal (pf., Text-fig. 5) (P. 44943–44) leading forwards towards the oculomotor notch ; this small canal must have transmitted the profundus nerve, and indicates that this nerve normally emerged through the trigeminal foramen. In P. 44940 there is a separate foramen for the profundus nerve in front of the trigeminal foramen. The abducens nerve passed ventrally into the myodome through a small foramen (VI, Text-fig. 5 ; Pl. 3, fig. 8) in the prootic bridge. Behind the internal openings of the trigeminal and facial foramina there is a large recess on the internal face of the prootic which housed the ampullae of the anterior and external semicircular canals, and the anterior part of these canals was enclosed within the prootic lateral to this chamber (a.s.c., Pl. 3, fig. 8) (P. 44934).

The mydome (myo., Text-fig. 5) is wide at its orbital opening, but tapers rapidly and ends at the posterior edge of the prootic, without entering the basioccipital. The floor of the myodome is formed by the parasphenoid. The myodome does not open posteriorly.

The otolith chamber is large, with a rather strongly inflated lateral wall (Text-figs. 3, 4, 5), and extends to the ventral edge of the prootic and basioccipital, though it is closed ventrally by these bones and not by the parasphenoid. The chamber communicates with the cranial cavity above through a very large oval fenestra (f.o.c., Pl. 3, fig 8).

The basisphenoid (bs., Text-figs. 2, 5) (P. 44930–33) has a short, stout pedicel which is inserted ventrally on the hind edge of the median crest on the parasphenoid, and a pair of short, slender arms which meet the edge of the prootic bridge, enclosing the pituitary fossa between them. The pedicel of the basisphenoid contains a pair of canals (c.i.c.a., Text-fig. 5) which transmitted the internal carotids upwards, and the arteries probably entered the cranial cavity through the wide optic fenestra (II, Text-fig. 5).

The pleurosphenoid (pls.) (P. 44940–45) is a moderately large plate of bone which meets the frontal and autosphenotic dorsally, the orbitosphenoid anteriorly and the prootic behind, and is separated from its fellow by the optic fenestra. The posterior part of the bone bears a low ridge which is continuous with the ridge on the orbital face of the prootic. Below this ridge the bone contains a foramen (f.a.c.v., Text-figs. 2, 3, 5) which probably transmitted the anterior cerebral vein. The trochlear nerve probably passed through the optic fenestra.

The orbitosphenoid (ors.) (P. 44946–47) is a large median bone, " V "-shaped in section, meeting the frontal above and the pleurosphenoid behind. The anterior margin of the optic fenestra is formed by a notch in the posterior edge of the bone. The antero-ventral edge of the bone bears a long median process which extended forwards almost as far as the hind edge of the lateral ethmoid. The olfactory nerves emerged through a large foramen (I) above the base of this process, and ran forwards along the dorsal edge of the process. In the centre of the lateral face of the orbitosphenoid there is a large oval fenestra (Text-figs. 2, 3 ; P. 44948).

(c) *Cheek and Upper Jaw*

In most of the more or less complete specimens the bones of this region are badly crushed. The fragmentary material from Lulworth, on the other hand, contains many fine examples of individual bones but these are detached from one another and from the neurocranium. Fortunately we were able to prepare one of the more complete specimens (P. 1073) to show the inner surfaces of some of the cheek bones (Pl. 1, fig. 2), and, using mainly this specimen and the isolated bones from Lulworth, it has been possible to make a fairly accurate reconstruction of this part of the skull (Text-fig. 6).

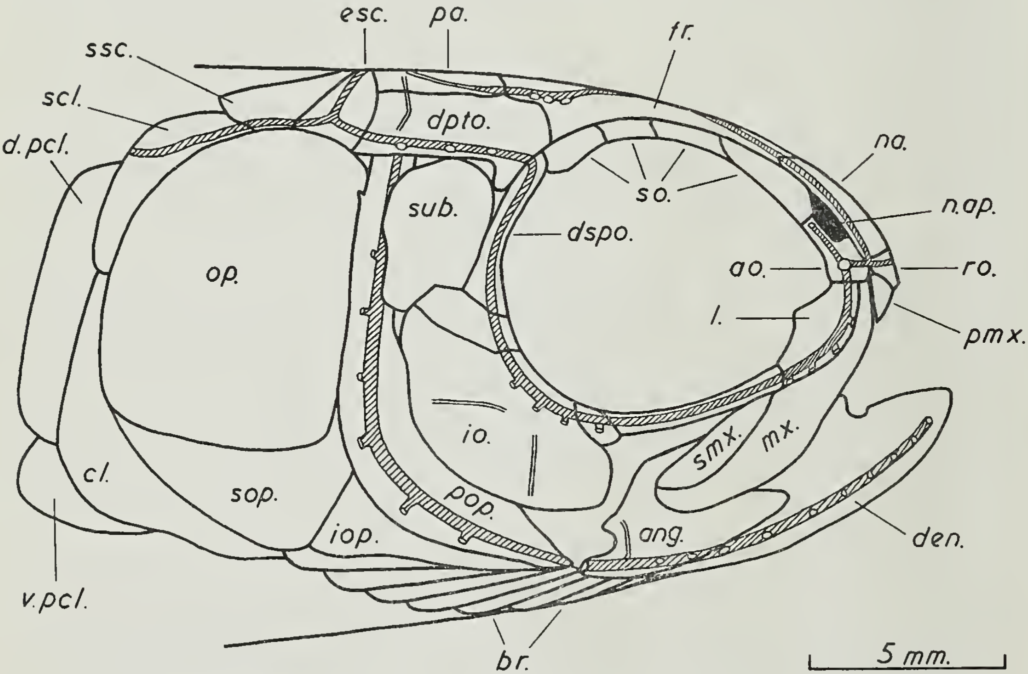

FIG. 6. *Ichthyokentema purbeckensis.* Reconstruction of skull and pectoral girdle in lateral view. For explanation of lettering see p. 43.

The opercular series consists of the opercular, subopercular, interopercular and the branchiostegal rays. The opercular (op.) is a large bone, roughly one and a half times as high as it is long. Its strongly curved dorsal and posterior border overlaps the dermal bones of the pectoral girdle, the nearly straight ventral border overlies the dorsal part of the subopercular, and the sinuous, thickened, anterior border is in turn covered by the preopercular. The ventral edge of the opercular lies approximately at right angles to the anterior edge. The articular facet for the hyomandibular lies near the anterior margin and roughly one-third of the distance from the dorsal to the ventral edge ; in some specimens its position is indicated by a small, rounded projection of the anterior margin. The external surface of the bone bears faint, concentric growth lines but is otherwise smooth.

The subopercular (sop.) is considerably smaller than the opercular. The part of the bone exposed on the surface of the skull was roughly triangular ; the anterior part of the dorsal margin is produced into a long, tapering, vertical process, nearly equal in height to the remainder of the bone, but this was completely concealed beneath the opercular and preopercular.

The interopercular (iop.) is a long, triangular bone lying in front of the subopercular and overlain dorsally by the preopercular. In P. 7640 the remains of five slender branchiostegal rays (br.) can be seen lying ventral to the interopercular. A broad median gular plate (g.p., Text-fig. 7) is present in P. 40635.

The preopercular (pop.) is long and curved. The ventral part of the bone is slightly expanded and strongly curved, with its lower end directed forwards. The dorsal part is narrower, straighter, and nearly vertical in position ; its upper end abuts against the dermopterotic. The curved postero-ventral border overlies the bones of the opercular series, the antero-dorsal edge is partly covered by the suborbital and the second infraorbital. The preopercular sensory canal ran through the bone giving rise to a number of short lateral branches along its posterior and ventral edges, and then continued on to the mandible.

The dermal bones surrounding the orbit are : the supraorbitals, the dermosphenotic, the infraorbitals, the lachrymal and the antorbital, which together form a complete ring around the orbit ; and the suborbital, which lies immediately behind the dermosphenotic. In P. 1073 a chain of four supraorbitals (so.) can be seen. The first is small, unusually thick, and in contact posteriorly with the dermosphenotic. The next two are thinner, the second is shorter than the first and the third longer. The fourth supraorbital is nearly as thick as the first and more than twice its length. It is in contact antero-dorsally with the frontal and nasal, antero-ventrally with the antorbital and its anterior edge contributes to the border of the nasal aperture. The first and second supraorbitals bear elongated tubercles of ganoine on their external surfaces ; the third and fourth are known only from the internal surface. The dermosphenotic (dspo.) is a slightly curved, almost cylindrical bone, lying vertically with its upper part in contact with the front edge of the dermopterotic. The main cephalic sensory canal entered a little distance below the upper end of the bone, bent through a right angle, and continued parallel to the long axis of the bone as the infraorbital canal. In P. 1073 there are four infraorbitals (io.). One of these, the second counting from the dermosphenotic, is considerably larger than the others and partly overlies the preopercular. On the external surface of the second infraorbital can be seen the horizontal and vertical pit-lines of the cheek. The presence of these pit-lines on the second infraorbital of an undetermined species of *Pholidophorus* from the Lias of Lyme Regis has been recorded by Westoll (1937 : 376). The fourth infraorbital is a long slender bone. The lachrymal (l.)

bears a small facet for articulation with the lateral ethmoid. On its external surface, postero-dorsal to the sensory canal, the lachrymal bears a curved row of five prominent spines (P. 44978–79) ; P. 44979 bears in addition three or four small raised tubercles. The infraorbitals and the lachrymal contained the infraorbital sensory canal which gave off several short branches directed away from the orbit ; the second and third infraorbitals and the lachrymal bearing three or four, one, and four such branches respectively. The antorbital (ao.) is a small bone containing the junction of the infraorbital and ethmoid sensory canals, and a short branch which extends postero-dorsally parallel to the supraorbital canal and ends just within the bone in a pore to the surface (P. 3607 ; P. 45020). A second pore opens directly into the junction of the three canals. The dorsal border of the antorbital bears a semicircular notch which forms the ventral edge of the narial opening. The bone is ornamented externally with two or three small spines. P. 1073 shows a single suborbital bone (sub.) of irregular shape lying immediately posterior to the dermosphenotic and first infraorbital.

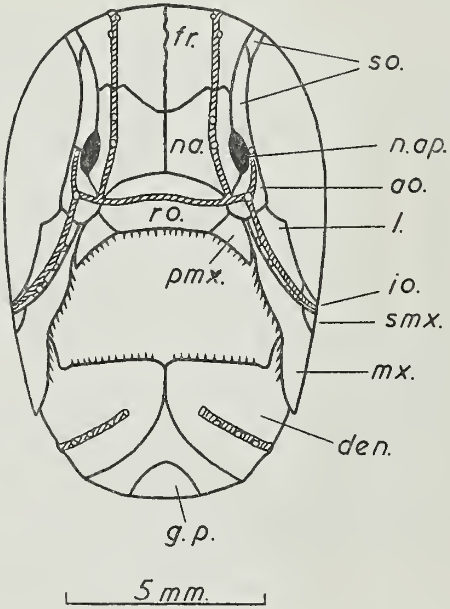

Fig. 7. *Ichthyokentema purbeckensis.* Reconstruction of the skull in anterior view. For explanation of lettering see p. 43.

Part of a bony sclerotic ring can be seen in P. 8378 and the material from Lulworth includes several isolated examples. As far as can be ascertained the sclerotic ring was a continuous structure and not divided into a number of separate ossifications.

The upper jaw contains the premaxilla, maxilla and one supramaxilla. The bones are shown in lateral view in Text-fig. 6.

The premaxilla (pmx., Pl. 2, fig. 5) (P. 8379 ; P. 44956) is a small, roughly triangular bone bearing about ten teeth in a single row along its oral border. The premaxillae did not meet in the mid-line, but were separated by the rostral. A small notch on the medial edge of the premaxilla articulated with a projection on the lateral edge of the rostral. A projecting facet in the centre of the dorsal edge of the premaxilla articulated with the antero-ventral corner of the antorbital.

The maxilla (mx.) (P. 1073 ; P. 44957) is rather short, and ends below the centre of the orbit. The bone bears a single row of teeth which extends along the entire length of its oral border. The rod-like head of the maxilla inclines medially at about 45 degrees to the body of the bone, and articulated with a facet at the base of the wing of the vomer. The premaxilla lay below and in front of the head of the maxilla. A slight thickening of the dorsal surface of the lateral part of the head of the maxilla marks the articulation of the maxillary process of the palatine. The maxilla is unornamented.

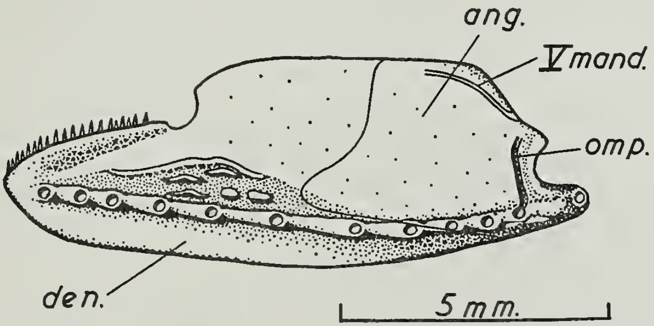

Fig. 8. *Ichthyokentema purbeckensis.* Reconstruction of left mandible in lateral view. Based mainly on P. 44973–75 and P. 45031. For explanation of lettering see p. 43.

The single supramaxilla (smx.) (P. 7807 ; P. 3607 ; P. 44958) is an elongated slip of bone, pointed anteriorly, whose curved ventral edge fits against the dorsal part of the posterior half of the maxilla.

(d) *Mandible*

The lower jaw is composed of four elements : the dentary and angular, which together form the entire external or labial surface of the mandible ; the Meckelian bone ; and a single small coronoid (Text-figs. 8, 9 ; Pl. 4, fig. 9).

The dentary (den.) is the largest of these four bones. It is gently curved in the vertical plane so that the inner surface is concave and the outer convex ; in addition the anterior part of the bone shows a strong curvature in the horizontal plane towards the mid-line. From the anterior end of the dentary the dorsal margin is thickened for slightly less than half its length and this region bears teeth. In P. 12515 and P. 7640 these teeth can be seen as simple, conical structures from 0·6 to 0·8 mm in height. In the isolated mandibles, P. 44973–75, though the teeth themselves are missing their attachments to the jaw can be seen ; there appear to have been between 20 and 30 teeth arranged two or three deep along the edge of bone. The dentigerous part of the dorsal margin is separated from the moderately well developed coronoid process by a small, rounded notch. The anterior and ventral edges of the bone are both gently curved. Posteriorly the dentary is in contact with the angular and extends backwards for a considerable distance ventral to that bone. A little distance above the ventral margin of the dentary, and lying roughly parallel to it, is the tube which contained the mandibular sensory canal. The canal was enclosed in a rather thicker portion of the bone so that this region is raised slightly above the general level of the external surface of the mandible. The canal gave off about twelve branches through pores along its length. Dorsal to the canal a triangular area of the dentary bears a number of short ridges or elongate tubercles of bone. On the internal surface there is a low longitudinal ridge directly above which is a shallow depression. The ventral part of the Meckelian bone fits into this depression with its ventral edge abutting against the dorsal edge of the longitudinal ridge. The dentary is thickest in the tooth-bearing region of the dorsal margin and around and immediately dorsal to the sensory canal; thinnest on the coronoid process and near the ventral edge.

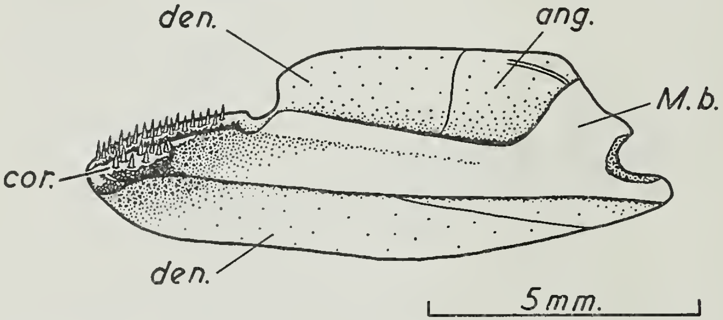

Fig. 9. *Ichthyokentema purbeckensis.* Reconstruction of right mandible in medial view. Based mainly on P. 44973–75. For explanation of lettering see p. 43.

The angular (ang.) joins with the dentary in the formation of the coronoid process. The anterior and most of the ventral border of the bone is in contact with the dentary and the dorsal edge is continuous with that of the latter. The posterior border of the angular slopes backwards and downwards with a prominent semicircular notch in the region of the jaw articulation. At the facet for the quadrate, although the angular and Meckelian bone are closely applied to each other, they are quite distinct, and the articular surface is formed by the Meckelian bone alone. In view of this the bone under discussion must be considered a true angular and is not an angulo-articular such as Rayner (1937 : 53) has described in *Leptolepis coryphaenoides.* The mandibular sensory canal entered the angular near its posterior end and ran forward into the dentary. On the whole the canal lay deeper in the bone than in the dentary so that the enclosing bone projects less above the general surface. A little distance in front of the articulation the angular bears a short vertical pit-line—the oralo-mandibular pit-line (omp.)—which communicates at its lower end with the sensory canal. The postero-dorsal part of the bone encloses a narrow, slightly curved canal (V mand.). Anteriorly the canal opens into a short groove on the external face of the angular, posteriorly by a foramen in the posterior edge of the bone a little distance above the jaw articulation. From its size and position it seems possible that this canal was traversed by a division of the mandibular branch of the fifth cranial nerve. On its internal surface the angular bears a continuation of the low, longitudinal ridge and shallow groove found on the dentary.

The Meckel's cartilage of the embryo has become ossified throughout its length to form a single continuous bone, without any sign of separate articular or mentomeckelian elements. This bone is referred to as the Meckelian bone (M.b.)—a term employed by Stensiö for the homologous structure in *Saurichthys ornatus* (Stensiö, 1925 : 107). The Meckelian bone is long and slender, and runs the whole length of the jaw. Posteriorly it is somewhat expanded, being developed into a coronoid process dorsally, and it forms the surface for articulation with the quadrate. In this region the bone is closely applied to the inner surface of the angular. Except for a small region near the extreme posterior end, the Meckelian bone lies with its ventral edge fitting into the shallow longitudinal depression in the angular and dentary and abutting against the longitudinal ridge which these bones bear. In the neighbourhood of the rounded notch in the dorsal edge of the dentary the Meckelian bone shows a similar notch or emargination in its dorsal edge. In front of this the bone tapers slightly, increases in thickness, and near and at the tip of the jaw becomes rolled upon itself so as to form an incomplete cylinder with unequally thickened walls and a small cavity which remains open on its medial side. Between the coronoid process and the rounded notch, the dorsal edge of the Meckelian bone is noticeably thicker than the very thin, more ventral portion. Apart from the contact between its ventral edge and the dentary and angular, the bone curves medially—away from the dermal bones. In the more anterior part of the jaw the bone lies close against the dentary and follows its curvature towards the median plane.

The single coronoid (cor.) is a small bone measuring only about 1·5 mm. in length, i.e. less than one-sixth of the length of the jaw. It lies in the anterior part of the jaw with its upper, tooth-bearing surface slightly below the level of the tooth-bearing region of the dentary. The dorsalmost part of its outer surface is in close contact with the inner surface of the thickened dorsal edge of the dentary ; the remainder of its outer surface fits into a shallow depression in the Meckelian bone. The coronoid bore about a dozen teeth. Two of the coronoid teeth can be seen in P. 44973 ; they are similar in structure and size to the teeth on the dentary.

(e) *Palate*

The palate is shown in medial view in Text-fig. 10. The hyomandibular (hm.) (P. 44950–51) is very broad, and lies almost vertically. The head of the bone is much broader than the facet on the neurocranium with which it articulates, and it must have been capped in life by a rounded mass of cartilage. The stout opercular process (op.p.) lies in the upper third of the bone. The ventral end of the bone is also broad, and this was capped by a mass of cartilage with which the interhyal articulated. On the upper part of the anterior edge of the hyomandibular there is a short process which inclines antero-ventrally towards a process on the metapterygoid. The hyomandibular trunk of the facial nerve entered a large foramen (VII hm.) near the anterior edge of the bone at the level of the opercular process, and passed ventrally in a groove on the lateral face of the bone. This groove is bounded anteriorly by a vertical ridge against which the anterior edge of the preopercular lay.

The symplectic (sym.) (P. 8379) is a rod of bone which tapers distally and is inserted in a groove on the medial face of the quadrate. The symplectic inclines forwards at about 45 degrees to the hyomandibular.

The quadrate (q.) (P. 44952–53) is the usual triangular bone, bearing a double condyle for the articular. This condyle lay below the posterior half of the orbit. The quadrate bears a posterior process which forms the hind edge of the groove lodging the symplectic. The anterior edge of the preopercular lay against the posterior edge of this process, and the retro-articular process of the mandible abutted against a thickening at the base of the process.

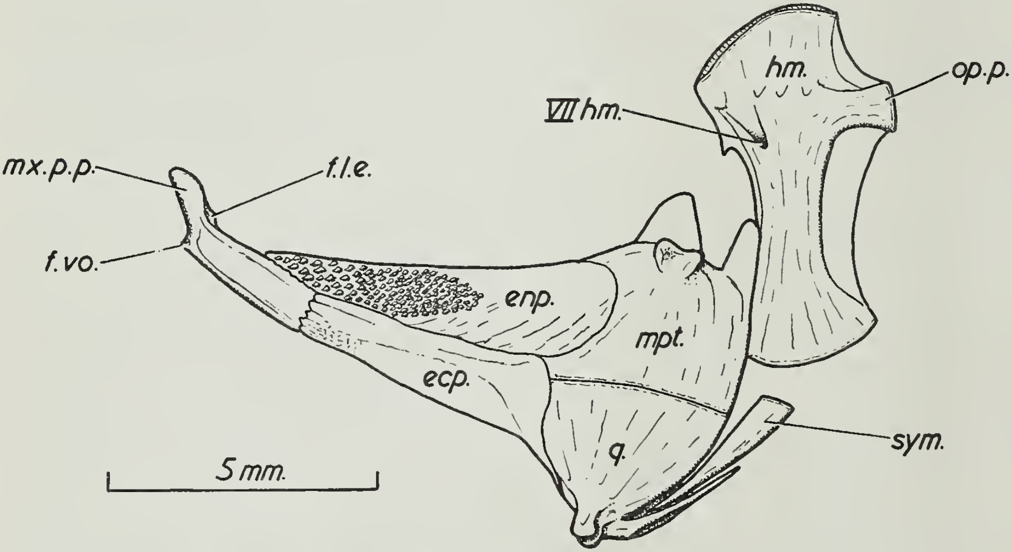

FIG. 10. *Ichthyokentema purbeckensis*. Reconstruction of palate of right side in medial view. For explanation of lettering see p. 43.

The metapterygoid (mpt.) (P. 44953–54) consists of a broad plate of thick cancellous bone bearing two processes and a condyle on its dorsal edge. The ventral edge of the bone met the quadrate in a close suture, with no intervening cartilage. The condyle projects medially, and articulated with the basipterygoid process of the parasphenoid. The anterior of the two processes is broad and delicate, and projects dorsally towards the short process on the anterior edge of the hyomandibular. The posterior process is strongly ossified, and projects dorso-laterally to meet the antero-lateral edge of the hyomandibular. The exact size of the anterior part of the body of the metapterygoid is not yet known, and it is uncertain if there was a fenestra between it and the hind edge of the ectopterygoid.

The endopterygoid (enp.) (P. 8378; P. 44955) is an elongated strip of bone which tapers anteriorly. The dorsal edge of the bone inclines medially, and met the edge of the parasphenoid. The ventral edge of the bone fits against the dorsal edges of the palatine and ectopterygoid, and the posterior part of the bone lies against the medial face of the metapterygoid. The anterior half of the endopterygoid is covered with teeth. These curve forwards a little, and grow smaller posteriorly, as they do on the parasphenoid.

The ectopterygoid (ecp.) (P. 44956–57) is bent through about 45 degrees. Its tapering posterior limb meets the anterior edge of the quadrate and its long, stout anterior limb meets the palatine. At the postero-dorsal corner of the anterior limb of the bone there is a flange which lies medial to the quadrate and metapterygoid. The ectopterygoid bears no teeth, but the antero-ventral corner of the medial face of the bone is roughened.

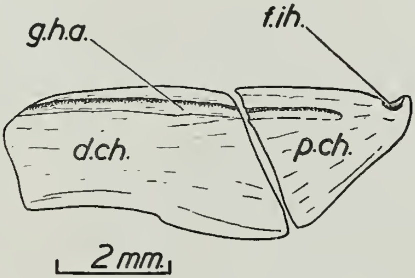

FIG. 11. *Ichthyokentema purbeckensis*. Reconstruction of left ceratohyal in lateral view. For explanation of lettering see p. 43.

The palatine (P. 7640; P. 44958–59) is a small, elongated bone bearing a stout maxillary process (mx.p.p.) anteriorly. The maxillary process articulated with the dorsal surface of the proximal part of the maxilla. Saint-Seine (1949 : 301) speaks of a maxillary process on the palatine as being characteristic of the teleostean family Chirocentridae, and states that the presence of the process in *Thrissops* is an advanced character which foreshadows the chirocentrids. In fact, a maxillary process occurs on the palatine of almost all teleosts, and is not particularly characteristic of chirocentrids. The presence of a maxillary process in *Ichthyokentema* suggests that the process was probably present in most halecostomes. The palatines of *Pholidophorus* and *Leptolepis* are not well known, and the process may well have been present in them. The projecting antero-ventral edge of the palatine (f.vo.) articulated with the edge of the vomer, and a facet (f.l.e.) on the dorsal surface of the base of the maxillary process articulated with the cartilage capping the ventral edge of the lateral ethmoid. The palatine bears no teeth, but the bone appears to be entirely cartilagenous in origin, and it is possible that a toothed dermopalatine was loosely attached to its oral border.

(f) *Branchial Skeleton*

The skeleton of the hyoid and branchial arches is still very poorly known. The only part of the hyoid arch seen is the ceratohyal (Text-fig. 11 ; P. 44971–72). The ceratohyal is ossified in two pieces. The triangular proximal ossification (p.ch.) bears a facet (f.ih.) for the interhyal at its postero-dorsal corner. The distal ossification (d.ch.) is rectangular, and is not perforated by a fenestra as it is in *Leptolepis* (Rayner, 1937 : 55). A groove (g.h.a.) for the afferent pseudobranchial artery crosses the lateral faces of both ossifications, and ends in front of the facet for the interhyal.

The branchial arches are known only by fragments, but the holotype shows that the first arch bore small teeth.

(g) *Axial Skeleton*

None of the material shows the vertebral column in its entirety. Three of the more complete specimens show a few vertebrae but the structure of the vertebrae can best be seen in some of the isolated specimens from Lulworth. The vertebral centra are thin cylinders of bone, almost invariably greater in diameter than in length (Text-fig. 12) ; out of approximately 90 vertebrae examined, in one only was the length of the centrum as great as its diameter. The anterior and posterior ends of the centrum are irregular and somewhat variable, though on the whole they tend to be arranged so that the length of the centrum is noticeably less dorsally than ventrally. Each neural arch (neu.) consists of a pair of structures attached at their lower ends to the dorsal or dorso-lateral surfaces of the centrum. The two halves of the neural arch are inclined backwards and meet each other a little distance above the centrum ; they are quite firmly attached in this region though they can still be distinguished by the presence of superficial grooves and a change in the appearance of the bone. The region dorsal to the neural canal is preserved in only a small number of specimens. In some of these (P. 44976 ; P. 45021) the two halves of the neural arch appear to be continuous with a neural spine which is obviously of double origin but with the two halves firmly fused, in two other specimens (P. 45022–23) immediately dorsal to the neural arch lies an expanded portion of the bone with a hemispherical or cup-shaped socket which presumably served for the articulation of a neural spine. One of these specimens (P. 45023) appears to be from the caudal region, the other (P. 45022) may possibly be from the abdominal region ; they may both have lain in the region of the dorsal fin. In the abdominal region each vertebral centrum bears a pair of short transverse processes (t.p.) arising from its ventro-lateral surfaces, each transverse process having an articulating surface for the head of the pleural rib (Text-fig. 12) (P. 45024). In the caudal region the transverse processes extend downwards and meet beneath the centrum to form the haemal arch. The two processes fuse and are then continued ventrally as a haemal spine, obviously of double origin, in a manner analogous to the neural spine born dorsally (P. 45021). It was impossible to ascertain the total number of vertebrae present in one individual.

Portions of seven or eight curved ribs can be seen in the anterior trunk region of

P. 8378, and fragments of similar ribs have been observed in the material from Lulworth ; in P. 8378 they appear to have been about 5·5 mm. in length.

No traces of intermuscular bones have been found and it seems probable that none was present.

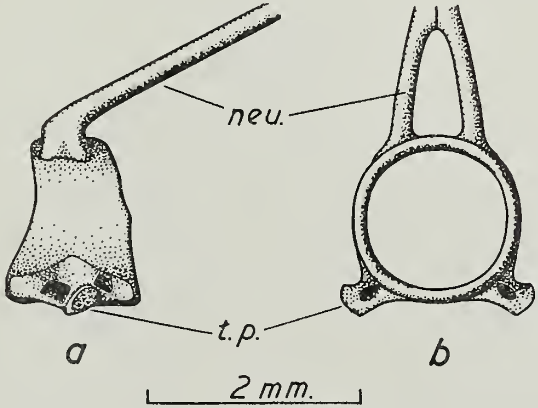

FIG. 12. *Ichthyokentema purbeckensis.* Reconstruction of trunk vertebra. *a*, in lateral view, *b*, in anterior view. Based mainly on P. 44976 and P. 45024. For explanation of lettering see p. 43.

(h) *Appendicular Skeleton*

The pectoral girdle is shown in lateral view in Text-fig. 6 and in medial view in Text-fig. 13.

The extrascapular (esc.) (P. 44963) is a triangular bone, tapering to a point medially. It is uncertain whether or not it met its fellow in the mid-line. The lateral line canal entered the postero-lateral corner of the bone from the suprascapular, and divided immediately within the bone into the main cephalic canal which passed forwards into the dermopterotic, and the supratemporal commissural canal which passed medially, giving off three or four branches through small pores en route.

The suprascapular (ssc.) (P. 44964) is large, and roughly equal in size to that of *Pholidophorus similis* (Saint-Seine, 1949 : 217). The bone may possibly have met its fellow in the mid-line, and its straight anterior edge fitted against the posterior edge of the extrascapular. The antero-lateral corner of the bone is thickened, and bears a slender process which passes antero-ventrally and was bound to the intercalar by ligaments. The lateral line canal, received from the supracleithrum behind, passed forwards to the extrascapular through a short canal at the extreme lateral edge of the bone. The surface of the suprascapular is ornamented with feeble ridges.

The supracleithrum (scl.) (P. 6171 ; P. 44965) is a blade-shaped bone with a thickened anterior edge. The head of the bone bears two projections which articulate with notches on the hind edge of the suprascapular. The lateral line canal, received posteriorly from the anterior lateral line scale, passed antero-dorsally through the bone and emerged immediately below the lower of the two projections on the head of the bone. The surface of the supracleithrum is ornamented with feeble ridges.

The cleithrum (cl.) (P. 44966) is the usual large sigmoid bone. The anterior edge of the bone is thickened, and from the middle part of it a flange extends antero-medially to form the hind edge of the opercular opening. Dorsally the bone tapers to a point which lay medial to the ventral end of the supracleithrum. The exposed lateral face of the cleithrum is ornamented with a few vertical ridges.

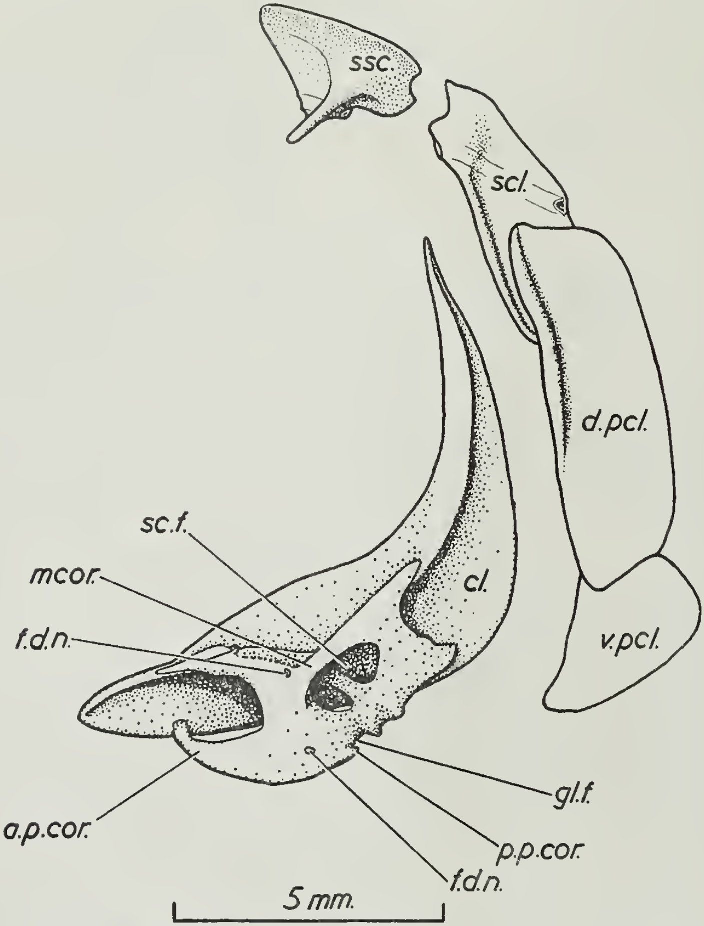

Fig. 13. *Ichthyokentema purbeckensis.* Reconstruction of pectoral girdle of right side in medial view. The supracleithrum and postcleithra are displaced posteriorly. For explanation of lettering see p. 43.

The endoskeletal pectoral girdle (Pl. 4, fig. 10) (P. 44966–68) is ossified in a single piece, with no sign of sutures between the scapular, coracoid and mesocoracoid elements. There is a very large scapular foramen (sc.f.) in the centre of the scapular region, and the foramen is divided horizontally by a strut of bone which passes antero-laterally and attaches to the cleithrum. The glenoid facet (gl.f.) on the hind edge of the girdle inclines ventro-medially at about 45 degrees. The facet was covered in life by cartilage, and it is limited below by a very short posterior process of the coracoid (p.p.cor.). Above the glenoid facet the scapula bears a prominent saddle-shaped facet with which the anterior rays of the fin articulated, as in teleosts. A moderately stout mesocoracoid arch is present (mcor.), arching vertically over the medial face of the scapular foramen. The coracoid has a slender anterior process (a.p.cor.) which arches antero-ventrally and attaches to the lateral edge of the cleithrum some distance above the tip of the latter. The coracoid is pierced by three foramina (f.d.n.) which probably transmitted diazonal nerves, one lying at or near the junction of the bone with the cleithrum, one lying just in front of the base of the mesocoracoid arch and one lying near the posterior edge of the bone.

There are two postcleithra. The dorsal postcleithrum (d.pcl.) (P. 1073 ; P. 44969) is a large, rectangular bone lying medial to the supracleithrum and the dorsal part of the cleithrum and bearing a short flange which projects medially from its anterior edge. The ventral postcleithrum (v.pcl.) (P. 1073 ; P. 44670) is a trapezoid bone lying medial to the middle part of the cleithrum and the upper edge of the endoskeletal girdle. At the antero-dorsal edge of the bone there is a short pointed process which fits against the antero-ventral corner of the dorsal postcleithrum.

The radials of the pectoral fin are known only by very incomplete fragments, and their number is not known.

The pectoral fins are, at best, poorly preserved. They appear to have contained at least 11 rays, the first of which is stouter than the remainder. In specimen P. 8379 traces of fulcral scales can be seen lying along the anterior face of the first fin-ray. some, at least, of the rays were jointed and may have branched.

The pelvic girdle is not known but the pelvic fins are on the whole slightly better preserved than the pectoral. They are a little smaller than the latter and contained more than five rays, the first of which bears five or six fulcral scales. All the rays are jointed and all except the first branch distally.

The dorsal fin is roughly triangular in shape and contained nine rays. All the rays are jointed and branched. The first fin-ray is bordered by six fulcral scales and these are preceeded by two basal fulcra.

The endoskeleton of the anal fin can be seen in specimens P. 7640, P. 12515 and P. 8378. In P. 7640 six radials are exposed. The first of these lies opposite the base of the first fin-ray, the second lies close to the first and resembles it in length and stoutness, the remainder are rather more widely spaced and decrease gradually both in length and in thickness. In some specimens traces of the radials of the dorsal fin can be observed but these are not so well exposed as those of the anal fin just described.

The anal fin is approximately equal in size to the dorsal and closely resembles it in shape and construction. It contained seven rays in P. 8378 and six rays in P. 7640. As in the dorsal fin there are six fringing fulcra and two basal fulcra.

The caudal fin is bilobed and roughly symmetrical apart from the presence of a small scale-covered lobe of the body that extends dorsally for about one-third of the distance to the tip of the epicaudal lobe. Nothing can be seen of the endoskeleton of the caudal fin. In P. 8378 the fin contains 19 principal rays, 17 of which are branched. The outermost ray of the upper lobe bears about ten fulcra, grading into the dorsal ridge scales anteriorly. The outermost ray of the lower lobe bears eight fulcra, and is preceded by three short, jointed, but unbranched rays, the last of which bears one fulcral scale.

(j) *Squamation*

The squamation has been described in detail by Smith Woodward (1919 : 110) and, apart from details of the internal structure of the scales, little can be added to his account

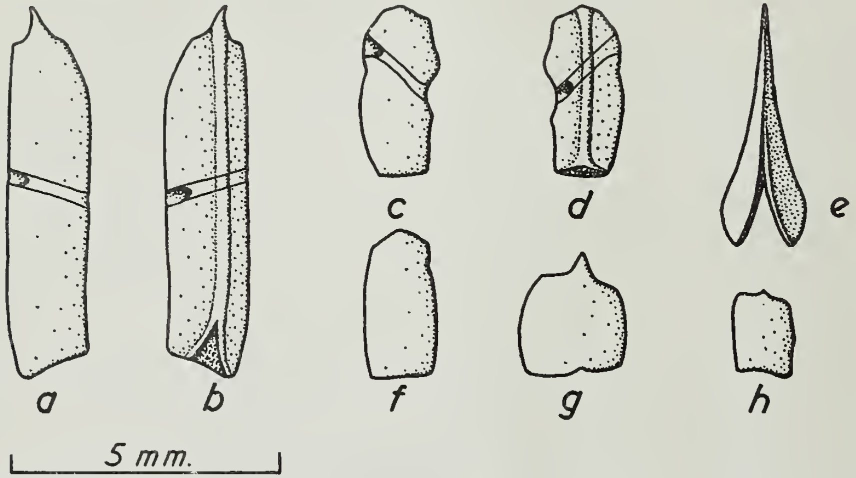

Fig. 14. *Ichthyokentema purbeckensis.* Unrestored drawings of scales : *a*, anterior scale of lateral line series in external view, from P. 45025 ; *b*, same scale in medial view ; *c*, posterior scale of lateral line series in external view, from P. 45026 ; *d*, same scale in medial view ; *e*, dorsal or ventral ridge scale from caudal peduncle, external surface, from P. 45027 ; *f*, scale from posterior trunk or anterior caudal region adjacent to lateral line series in lateral view, from P. 45028 ; *g*, scale from anterior trunk region towards dorsal or ventral mid-line, external surface, from P. 45029 ; *h*, scale from caudal region in lateral view, from P. 45030. In *a–d*, *f–h* dorsal is towards the top of the page ; anterior is to the left in *a*, *c*, *f*, *g* and *h* ; to the right in *b* and *d* ; and towards the bottom of the page in *e*.

The scales are of moderate thickness, the external surfaces are smooth and the posterior edges without serrations. They are strengthened on their inner surfaces by a conspicuous vertical ridge (Text-fig. 14*b*, *d*). The scales of the trunk region articulate by a peg-like projection of the upper edge fitting into a V-shaped depression in the inner face of the lower part of the scale above (Text-fig. 14*a*, *b*, *g*). In the caudal region this articulation is considerably reduced in extent (Text-fig. 14*c*, *d*) or altogether absent. There appear to be nearly forty obliquely vertical rows of scales. In the anterior trunk region the scales of the lateral line series are very deep relative to their length, the ratio of scale height to length being as high as 4·1 to 1 in the region immediately behind the pectoral girdle. The relative height of the scales decreases gradually as this series is traced back to the tail region and more rapidly along each of the obliquely vertical rows as one gets further from the lateral line. Near the dorsal and ventral surfaces in the trunk region, and in the caudal region the scales are approximately diamond-shaped (Text-fig. 14*g*, *h*). The caudal fin is preceded dorsally and ventrally by a small number of ridge scales (Text-fig. 14*e*), but these are not especially conspicuous. A few slightly enlarged, rounded scales lie in or near the mid-line a little distance anterior to the anal fin ; in specimen P. 8378 one of these scales shows two denticulations posteriorly.

The scales are of the " lepidosteoid " type (Goodrich, 1908 : 758). Externally there is a well marked layer of enamel or ganoine which forms approximately one-tenth of the total thickness of the scale. The remainder of the scale consists of bone. This contains numerous, well developed and evenly distributed cell spaces and the canals of Williamson (Pl. 2, fig. 6). The latter are not particularly numerous and rather narrow ; they end a little distance below the ganoine layer.

V. DISCUSSION

(a) *The systematic position of the genus* Ichthyokentema

In 1941 A. S. Woodward split the genus *Pholidophorus* Agassiz into four. Some species were retained within the genus, the remainder he distributed amongst three new genera—*Pholidophoroides*, *Pholidophoristion* and *Ichthyokentema*. Woodward's new genus *Ichthyokentema* contained only *I. purbeckensis* (Davies) and *I. brevis* (Davies) ; in our opinion *I. brevis* is a synonym of *I. purbeckensis* (see p. 7). In the case of *Ichthyokentema* Woodward justified the erection of a new genus on the grounds that in it the lateral line scales are relatively deeper, and the fulcra and the dorsal and anal fins are relatively larger than in his restricted genus *Pholidophorus*. Woodward's splitting of the genus *Pholidophorus* has not generally been accepted, and has been criticized by Saint-Seine (1949 : 29), rightly in our opinion, as being based on insufficient characters. However, the present description of *Ichthyokentema* shows that Woodward was correct in erecting this genus, though the characters which distinguish it from *Pholidophorus* are more numerous and of greater importance than those he mentioned. His other two genera—*Pholidophoroides* and *Pholidophoristion*, have not been investigated, and as the structure of the species allocated to them is only poorly known they will not enter into this discussion.

Of the many species of *Pholidophorus* known, only the Liassic *P. bechei* Agassiz (the type species) and the Kimeridgian *P. similis* A. S. Woodward, both included by Woodward in his restricted genus *Pholidophorus*, have been described in detail; the former by Rayner (1948 : 318) and the latter by Saint-Seine (1949 : 215). If correctly interpreted by these two authors, it seems unlikely that the two species can be congeneric, for, according to Saint-Seine, in *P. similis* the supraorbital sensory canal passed from the nasal into the rostral, and there was no connection between the dorsal branch of the infraorbital canal in the antorbital and the supraorbital canal, while, according to Rayner, in *P. bechei* the supraorbital canal from the nasal connected with the dorsal branch in the antorbital, and the supraorbital canal had no connection with the ethmoid commissure. Of these two arrangements, that in *P. similis* agrees with the conditions in the parasemionotids and in *Ichthyokentema*, and it seems possible that the structure of *P. bechei* has been misinterpreted. Assuming this to be so for the present discussion, *Ichthyokentema* differs from *Pholidophorus* as represented by *P. bechei* and *P. similis* in the following characters :

1. The presence of teeth on the rostral and the separation of the premaxillae by this bone.
2. The broad median contact between the nasals, with little or no separation of the nasals by the frontals.
3. The large number (four) of supraorbitals.
4. The presence of a toothed coronoid and a fully ossified Meckelian bone in the mandible (Rayner (1948 : 319) mentions a separate prearticular in *P. bechei*, but this bone bore no teeth, and may represent part of the Meckelian bone).
5. The presence of an oral pit-line on the mandible.
6. The presence of a strong dentition on the vomer, parasphenoid and endopterygoid.
7. The absence of an aortic groove or canal below the occipital region of the neurocranium.
8. The pedicel of the basisphenoid is stout and contains a pair of canals for the internal carotid artery.
9. The suture between the opercular and subopercular is almost horizontal in *Ichthyokentema*, but is strongly inclined in *Pholidophorus*.
10. The presence of two postcleithra (only one postcleithrum is known in *Pholidophorus*, but a second one was possibly present since it occurs in both the parasemionotids and the teleosts).

With the exception of the toothed rostral, all these differences are relatively minor, and there is a large number of important characters which *Ichthyokentema* shares with both *Pholidophorus* and *Leptolepis*, showing that *Ichthyokentema* is undoubtedly a member of the Halecostomi. These halecostome characters[1] include the pattern of the sensory canals on the skull roof, the large dermopterotic, the presence of a large supraoccipital and autopterotic, the absence of a surangular in the mandible, the single suborbital, the well ossified vertebrae and the form of the caudal fin. The rhombic scales, with peg and socket articulations, a layer of ganoin, and with bone cells and canals of Williamson (cf. *Pholidophorus higginsi* (Gardiner, 1960 : 317)), and the fulcral scales place *Ichthyokentema* in the Pholidophoriformes rather than in the Leptolepiformes.

Ichthyokentema is therefore a member of the Pholidophoriformes which differs from the Pholidophoridae in one important feature, the toothed rostral separating

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[1] While discussing the characters of Halecostomi, it should be mentioned that the characters of this group listed by Saint-Seine (1949 : 299) include, in contrast to holosteans, the general absence of a basipterygoid process, the absence of a gular and the general absence of suborbitals ; and, in contrast to teleosts, the presence of an extrascapular. In fact, none of these characters is typical of halecostomes. The only halecostome in which the basipterygoid process is definitely lost is *Eoprotelops* (Saint-Seine, 1949 : 262) ; a gular is apparently always present in halecostomes (pholidophorids, leptolepids, oligopleurids, archaeomenids, *Ichthyokentema*) ; a single suborbital is present in all halecostomes in which the cheek is known except *Pholidophorus segusianus* (Saint-Seine, 1949 : 222), where it is fused with an infraorbital ; the extrascapular is present in all but a few specialized teleosts.

the premaxillae, and a number of less important characters including the extensive contact between the nasals, the four supraorbitals, the primitive mandible with a fully ossified Meckel's cartilage, a toothed coronoid and an oral pit-line, the strong palatal dentition, the angle of the suture between the opercular and subopercular and the form of the pedicel of the basisphenoid. All these characters are primitive (see below, p. 34), and *Ichthyokentema* could not therefore have evolved from the Pholidophoridae, yet its late age excludes it from the ancestry of the latter group. Thus *Ichthyokentema* must represent a phyletic line independent of the Pholidophoridae, and it must be placed in a separate family Ichthyokentemidae, defined as on p. 6 above.

(b) *The Origin and Evolution of the Halecostomi*

Ichthyokentema purbeckensis is only the third halecostome in which the neurocranium has been described, and in few halecostomes is the skeleton known in any detail. Detailed information on the structure of *I. purbeckensis*, especially on the characters in which it differs from *Pholidophorus*, make it necessary to discuss the history of the Halecostomi.

(i) *The Origin of the Halecostomi*

Gardiner (1960 : 347) has recently discussed the origin of the halecostomes (= Pholidophoroidea) and has produced much evidence indicating that the group originated from the Eotriassic Parasemionotidae (a family variously classed as advanced sub-holosteans or primitive holosteans), as had been suggested by Saint-Seine (1949 : 292) and by Schaeffer & Dunkle (1950 : 25). Gardiner mentions sixteen points of similarity between the Parasemionotidae and the Pholidophoridae (as represented by *Pholidophorus bechei* and *P. similis*). *Ichthyokentema* agrees with both the parasemionotids and pholidophorids in all these characters except the angle of the suture between the opercular and subopercular and the two postcleithra, in both of which it resembles the parasemionotids rather than the pholidophorids. The differences between *Ichthyokentema* and the Pholidophoridae are listed on p. 32 above. *Ichthyokentema* agrees with the parasemionotids in eight of these ten differences, the characters of the operculum and postcleithra mentioned above, the wide contact between the nasals, the large number of supraorbitals, the presence of a single coronoid and an oral pit-line in the mandible, the strong dentition of the palate, and the presence of canals for the internal carotids in the pedicel of the basisphenoid. *Ichthyokentema* differs from both the parasemionotids and pholidophorids in only one of the ten characters, the absence of an aortal groove or canal below the occipital part of the neurocranium. The major difference between the pholidophorids and *Ichthyokentema* is the presence in the latter of a toothed rostral which separates the premaxillae. Gardiner (in press) discusses the history of the bones of the snout in actinopterygians, and shows that the rostral, the premaxillae and the antorbitals are all derived from the rostro-antorbito-premaxillary of primitive palaeoniscoids such as *Stegotrachelus*, a bone which bears teeth, the rostral commissure and the junction between the supra- and infraorbital sensory canals. This single bone has fragmented in different ways in different lines, and has given rise to various combinations of snout bones. The presence in *Ichthyokentema* of a median rostral bearing both teeth and the ethmoid commissure is thus a primitive feature recalling the chondrosteans (though no chondrostean has yet been described in which there is both a toothed rostral and a pair of premaxillae). The condition in *Pholidophorus* and *Leptolepis*, with toothed premaxillae meeting beneath a toothless rostral, could be derived from the condition in *Ichthyokentema* by the premaxillae of the latter shifting medially until they excluded the rostral from the border of the mouth and so made its teeth redundant, or it could be derived independently from the primitive palaeoniscoid condition by the fragmentation of a toothed rostro-premaxillary. There is a third possibility, that the condition in *Ichthyokentema* was derived from that in *Pholidophorus* by the premaxillae shifting laterally so that the rostral entered the border of the mouth and acquired teeth secondarily. This must be discarded, firstly because there is no evidence that the rostral has ever acquired teeth secondarily, and secondly because there are eight characters in which *Ichthyokentema* resembles the parasemionotids and differs from *Pholidophorus*, and these eight characters must be taken to be primitive, while there is only a single character, the absence of an aortal canal, in which *Ichthyokentema* is more advanced than *Pholidophorus* ; the structure of the snout in *Ichthyokentema* is therefore much more likely to be primitive than it is in *Pholidophorus*. In the Parasemionotidae Lehman (1952 : 167) finds that some specimens of *Watsonulus eugnathoides* have a rostro-premaxillary and others have separate rostral and premaxillae, but does not say whether or not this rostro-premaxillary is paired or median. Piveteau (1941 : 73) describes a median rostral in *W. eugnathoides*, but is uncertain if the premaxillae are paired. In *Parasemionotus* Piveteau (1935 : 146) describes similar conditions, a median rostral and premaxillae which may or may not be paired. Thus it is still uncertain if there was a median rostro-premaxillary in the parasemionotids, but only if there was could both the pholidophorids and *Ichthyokentema* be derived from this family.

Leaving the structure of the snout aside, Gardiner (1960) has given a good account of how the halecostome viscerocranium could be derived from the parasemionotid, but he does not deal with the neurocranium. As *Ichthyokentema* is only the third halecostome in which the neurocranium is known, it is worth discussing some aspects of the evolution of the neurocranium in halecostomes. The parasemionotid neurocranium is known in *Ospia*, *Broughia* (Stensiö, 1932), *Parasemionotus* and *Watsonulus* (Lehman, 1952). The neurocrania of these four genera differ from those of the halecostomes *Pholidophorus*, *Leptolepis* and *Ichthyokentema* in the following characters.

1. The cranial fissure, absent in halecostomes, is present in all parasemionotids, though in *Ospia* both the vestibular fontanelle and the ventral part of the fissure (below the vagus foramen) are closed, and the fissure is not known to extend on to the roof of the neurocranium in any parasemionotid.

2. The parasemionotid neurocranium is normally ossified in a single piece, though in *Ospia* and *Watsonulus* there is the beginning of fragmentation into

separate bones with the separation of a basisphenoid and an orbito-pleurosphenoid in the hind wall of the orbit.

3. A fossa bridgei is present in the parasemionotids, and there is a spiracular canal opening into the floor of the fossa. In halecostomes there is no fossa bridgei or spiracular canal, but there is a large post-temporal fossa.

4. In parasemionotids the facial foramen did not open into the pars jugularis, but into the hinder part of the orbit, and the hyomandibular trunk of the facial nerve passed postero-laterally across the wall of the orbit to traverse the pars jugularis from end to end.

5. In parasemionotids the orbital artery was given off from the internal carotid after the latter had traversed its foramen in the parasphenoid (i.e. anterior to the ascending process of the parasphenoid), and the artery passed up through the myodome, entering the medial wall of the pars jugularis in *Parasemionotus* and *Watsonulus*, and failing to enter the pars jugularis at all in *Ospia*.

The first three of these five characters of parasemionotids are typical of chondrosteans, and give the neurocranium a palaeoniscoid appearance. The first two of the differences between parasemionotids and halecostomes are not of great importance, for the cranial fissure and vestibular fontanelle were evidently beginning to close in the parasemionotids, and in *Pholidophorus* the neurocranium is more or less completely ossified (Rayner, 1948 : 322). Rayner (1951 : 77) has suggested that closure of the cranial fissure in holosteans is associated with the increased mechanical function of the region of the neurocranium above the vagus foramen, where the intercalar and post-temporal fossa are developed. This is supported by the presence in *Pachycormus* of a cranial fissure (Lehman, 1949 : 29), as this fish is one of the very few holosteans in which the intercalar is not present.

The absence of a fossa bridgei and a spiracular canal in halecostomes is a real difference between them and the parasemionotids. The fossa bridgei is a depression in the dorsal surface of the otic capsule which lies lateral to the anterior and posterior semicircular canals and dorsal to the external semicircular canal, and is covered by the dermal bones of the skull roof. The fossa is present in all known chondrosteans, though in *Kentuckia*, the most primitive palaeoniscoid in which the neurocranium is known, the fossa is represented only by a group of pits (Rayner, 1951 : 78). The fossa is normally absent in holosteans. The function of the fossa is unknown, and in living chondrosteans it is filled with adipose tissue. Rayner (1951 : 79) has suggested that the fossa is functionless, but as Lehman (1958 : 2082) notes, the constancy of its structure is against this. The spiracular canal and the foramen of the otic branch of the facial nerve normally open into the floor of the anterior part of the fossa, and the foramen of the supratemporal branch of the glossopharyngeal nerve normally opens into its posterior part. The relationship between the fossa and the spiracular canal is not yet clear : Nielsen (1942, 1949) appears to hold that the depression on the roof of the neurocranium into which the spiracular canal opens is always part of the fossa bridgei, whether or not this depression is confluent with the main part of the fossa, while Rayner (1951) suggests that the spiracular canal is not necessarily associated with the fossa. There is a tendency for the fossa bridgei to divide into two in many chondrosteans ; in such forms the spiracular canal and the foramen of the otic nerve open into the anterior division of the fossa, and the foramen of the supratemporal nerve opens into its posterior division.

Stensiö (1925 : 27) has suggested that the fossa bridgei is homologous with the post-temporal fossa (temporal groove) of holosteans and teleosts. He is supported by Piveteau (1935 : 95). Stensiö was of the opinion that the fossa primitively housed the anterior epaxial trunk muscles, as does the post-temporal fossa, and that the muscles had secondarily withdrawn from the fossa in such forms as living chondrosteans and *Saurichthys*, where a large cranio-spinal process is developed for muscle insertion. This opinion is now untenable since in all the most primitive palaeoniscoids, where the cranio-spinal process is absent or very small, the fossa bridgei is closed posteriorly, and could not have served for muscle insertion. Topographically, the post-temporal fossa agrees almost exactly with the posterior division of the fossa bridgei : it lies lateral to the posterior semicircular canal, dorsal to the external semicircular canal, it is covered primitively by the dermal roofing bones, and often, as in *Ichthyokentema*, the foramen of the supratemporal branch of the glossopharyngeal nerve opens into its floor. Furthermore, no fish is known in which both the posterior division of the fossa bridgei and a well developed post-temporal fossa are present. In spite of these facts, it seems probable that the post-temporal fossa is a new formation which has displaced the fossa bridgei, and has not developed from the latter. Among parasemionotids, the course of the supratemporal nerve is known only in *Ospia* (Stensiö, 1932 : 237). In this genus the nerve, passing upwards from the glossopharyngeal foramen, perforated the lateral wall of the otic capsule to emerge in a shallow depression on the posterior face of the capsule, crossed this depression, and then perforated its roof to emerge in the posterior part of the fossa bridgei. The shallow depression on the posterior face of the otic capsule must, as Stensiö (1932 : 234) says, have served for the insertion of trunk muscles. In the advanced sub-holostean *Perleidus stoschiensis* the supratemporal nerve pursued a similar course (Stensiö, 1932 : 198). The depression on the hind wall of the otic capsule in *Ospia* and *Perleidus* has the same topographical relations as both the posterior part of the fossa bridgei and the post-temporal fossa (lateral to the posterior semicircular canal, dorsal to the external semicircular canal, and perforated by the supratemporal nerve) but it resembles the post-temporal fossa rather than the fossa bridgei in being open posteriorly and in having served for muscle insertion. The evidence suggests that the post-temporal fossa is derived from the shallow depression on the hind wall of the otic capsule of advanced sub-holosteans. Whether, as the post-temporal fossa increased in size by extending forwards, it became confluent with the fossa bridgei is not known, but Rayner (1951 : 78) thinks that the lateral cranial canal of the furid *Caturus*, a canal enclosed within the wall of the otic capsule and communicating with the cranial cavity, is derived from the posterior part of the fossa bridgei, which has already acquired a connection with the cranial cavity in the palaeoniscids *Pteronisculus* and *Boreosomus* (Nielsen, 1942). If this is so, one can imagine the post-temporal fossa increasing in size by pushing its anterior wall forwards, and so overgrowing and enclosing the posterior division of the fossa bridgei.

The anterior part of the fossa bridgei is normally associated with the dorsal opening of the spiracular canal. The spiracular canal is closed in all halecostomes and teleosts, but is open in the holosteans *Caturus* (Rayner, 1948 : 296), *Pachycormus* (Lehman, 1949 : 27) and *Amia*. The anterior division of the fossa bridgei has not yet been recognized in any holostean, but it is perhaps represented by the group of pits on the dorsal surface of the neurocranium of *Caturus* into which the spiracular canal opens (Rayner, 1948 : 296). Both the spiracular canal and the fossa bridgei were evidently lost very early in the halecostome line, but whether the loss of the fossa was associated with the closure of the spiracular canal is not yet known.

The fourth and fifth of the differences between the neurocrania of parasemionotids and halecostomes listed above appear to be due to specialization in the parasemionotids. In halecostomes, in teleosts, and in all known palaeoniscoids the facial foramen opens directly into the pars jugularis, and the hyomandibular trunk of the facial nerve traverses the jugular canal to emerge posteriorly either with the jugular vein or (primitively) through a separate lateral foramen. The condition in parasemionotids, where the hyomandibular trunk passed across the hind wall of the orbit (in *Watsonulus* the nerve passed through a secondary canal in this wall) before traversing the pars jugularis, is peculiar, and must be considered as a specialization. A similar arrangement occurs in the furid *Osteorachis* (Gardiner, 1960 : 287), and might support the derivation of furids from parasemionotids, but to derive the halecostomes from the parasemionotids makes it necessary to assume that in them the course of the hyomandibular trunk has reverted secondarily to the primitive palaeoniscoid type from the parasemionotid type.

The orbital artery in palaeoniscoids, in halecostomes (known only on *Ichthyokentema*), and in teleosts, leaves the internal carotid on the ventro-lateral face of the otic capsule, before the internal carotid passes through the parasphenoid (i.e. posterior to the ascending process of the parasphenoid), and passes dorso-medially to enter the pars jugularis, primitively passing through a separate foramen in the ventro-lateral wall of the latter, but never entering the myodome. The condition in parasemionotids, where the orbital artery was given off after the internal carotid had passed through the parasphenoid, traversed the myodome, and entered the medial face of the pars jugularis (or, as in *Ospia*, failed to enter the pars jugularis at all) must again be considered as specialized, and if we derive the halecostomes from the parasemionotids we must assume that the apparently primitive course of the orbital artery which they exhibit has been arrived at secondarily.

To sum up this discussion of the origin of the halecostomes, the parasemionotids are almost ideal intermediates between the chondrosteans and holosteans, but two features of the parasemionotid neurocranium, the course of the facial nerve and of the orbital artery, suggest that the group was not directly ancestral to the halecostomes. The snout of parasemionotids is not well known, but only if it contained a median rostro-premaxillary could the conditions in both *Pholidophorus* and *Ichthyokentema* be derived from it. If we accept that the parasemionotids were not directly ancestral to the halecostomes, it is no longer necessary to believe that the halecostomes did not appear until during or after the Eotrias, and it is then easier to account for the presence of the leptolepids, which are among the most advanced halecostomes, as early as the Middle and Upper Trias (Gardiner (personal communication) confirms that the Middle Triassic specimen mentioned by Rayner (1937 : 46) is indeed a leptolepid, and states that the age of *Leptolepis africana* Gardiner (1960 : 314) is definitely Upper Triassic).

(ii) *The Evolution of the Halecostomi*

Arambourg & Bertin (1958 : 2196) classify the Halecostomi in three orders, the Pholidophoriformes, Leptolepiformes and Aspidorhynchiformes. The aspidorhynchids are highly specialized forms which are not closely related to the other two orders (Gardiner, 1960 : 363), and whose origins are unknown : they may be left aside in the present discussion. The Leptolepiformes contains three families, the Leptolepidae, Oligopleuridae and Protelopidae. The derivation of the leptolepids from the Pholidophoridae is well established (Rayner, 1948 : 338). The Oligopleuridae and Protelopidae are not well known, but none of their known characters excludes the leptolepids from their ancestry, and at present the Leptolepiformes appears to be a monophyletic order derived from the Pholidophoridae. The Pholidophoriformes contains six families, the Pholidophoridae, Pleuropholidae, Archaeomaenidae, Ligulellidae, Majokiidae and Ichthyokentemidae. Detailed knowledge of the skeleton of *Ichthyokentema* makes it necessary to review the relationships of these families.

It is shown above (p. 34) that the structure of the snout in *Ichthyokentema* differs markedly from that of *Pholidophorus*, and that it is unlikely that the *Ichthyokentema* type of snout was derived from the *Pholidophorus* type because *Ichthyokentema* is more primitive than *Pholidophorus* in all but one of the characters in which it differs from the latter. The detailed similarities between *Ichthyokentema* and *Pholidophorus*, especially in those characters in which they both differ from the Parasemionotidae (ossification of the neurocranium in separate and identical bones, presence of a post-temporal fossa, absence of a spiracular canal and cranial fissure, structure of the cheek and vertebrae) make it unlikely that the two should have had an entirely separate origin. The evidence suggests, therefore, that despite its Purbeckian age, *Ichthyokentema* exhibits a primitive halecostome structure, especially in the snout, and that the pholidophorids must either have evolved from a Triassic form similar to *Ichthyokentema*, or have evolved independently from some form in the neighbourhood of the Parasemionotidae. Thus throughout the Jurassic there must have been two separate lines of halecostomes, one with a toothed rostral separating the premaxillae and one with a toothless rostral excluded from the border of the mouth by the premaxillae. It is worth examining the other four families of Pholidophoriformes to discover if any of them show signs of relationship to the ichthyokentemids rather than the pholidophorids.

The Pleuropholidae, a family characterized by deepening of the flank scales, duplication or triplication of the lateral line, and a small, toothless mouth which may have been protrusile, are described by Saint-Seine (1949 : 249 ; 1955 : 79). The family contains three genera, *Pleuropholis*, *Parapleuropholis* and *Austropleuropholis*. All three genera occur in freshwater deposits of Kimeridgian age in the Congo, and *Pleuropholis* also occurs in the marine Kimeridgian and the Lower Cretaceous of Europe. In *Parapleuropholis* Saint-Seine describes the snout as containing a toothed rostral, a postrostral bearing the ethmoid commissure, and a pair of nasals which are in contact in the mid-line. But since the bone which bears the ethmoid commissure is by definition a rostral, and since Saint-Seine saw no premaxillae, the conditions here suggest that the toothed bone is really the fused premaxillae. In *Pleuropholis*, Saint-Seine's account of the two species *P. thiolleri* and *P. janotti* shows marked differences in the snout. In *P. thiolleri* there is a pair of large, toothless premaxillae, a pair of small rostrals in which no sensory canal or pit-line has been seen, and a pair of nasals separated by the frontals. In *P. janotti* the nasals are separated by a median bone which Saint-Seine calls a postrostral, but no ethmoid commissure and no rostral or premaxillae have been seen. Similarly, in *Austropleuropholis* a postrostral is described, but no ethmoid commissure, rostral or premaxillae have been seen. Biese (1927 : 88) has described two species of *Pleuropholis* from the Kimeridgian lithographic stone of Bavaria. In *P. pompecki* he describes paired premaxillae, a median rostral (called the nasal) carrying the ethmoid commissure and paired nasals (called prefrontals) which are separated by the frontals. In *P. wagneri* he finds the same conditions except that the premaxillae are fused. The condition of the snout in the Pleuropholidae, so far as it is known, suggests that the family is derived from a pholidophorid type, with fusion of the premaxillae in *Parapleuropholis* and *Pleuropholis wagneri*, and fragmentation of the rostral in *Pleuropholis thiolleri*. None of the other known characters of the family is against its derivation from the pholidophorids.

The family Archaeomaenidae contains four genera, *Archaeomaene*, *Aphnelepis*, *Aetheolepis* and *Madariscus*, from Australian freshwater deposits of Jurassic age. The family is described by Wade (1941). Both Wade and Gardiner (1960 : 352) suggest that the family is derived from the Pholidophoridae, and this is borne out by the structure of the snout. The archaeomaenid snout is known in *Archaeomaene* and *Aphnelepis*, and in both genera there is a median rostral bearing the ethmoid commissure, the premaxillae are in contact below the rostral, and the nasals are in contact in the mid-line ; this is the typical pattern of the snout in a primitive pholidophorid. The four archaeomaenid genera appear to fall into two groups. In *Aetheolepis* and *Aphnelepis* the scales are rhombic and deepened on the flank (as in many species of *Pholidophorus*), and the second infraorbital below the dermosphenotic is enlarged (as in *Pholidophorus segusianus* (Saint-Seine, 1949 : 222), though the suborbital is here fused with the enlarged infraorbital). In *Archaeomaene* and *Madariscus* the scales are thin and cycloid, and the third infraorbital below the dermosphenotic is enlarged (as it is in *Pholidophorus bechei* (Rayner, 1948 : 320)). Unusual features of the Archaeomaenidae as described by Wade are the presence of a surangular in the mandible of *Aphnelepis* and the presence of a pit-line on the preopercular in *Archaeomaene*. Both these characters are typical of chondrosteans, and if they are in fact present would indicate that the archaeomaenids originated independently from forms like the parasemionotids, where a surangular and an unfragmented preopercular are still present.

The Majokiidae is a monotypic family containing *Majokia brasseuri* Saint-Seine (1955 : 107), a species known only by two specimens from the Kimeridgian freshwater beds of the Congo. Saint-Seine describes the snout of the species as containing a median rostral, a pair of lateral rostrals, a median postrostral and a pair of large nasals which are separated through the greater part of their length by the postrostral. No trace of the ethmoid commissure has been seen, and although toothed maxillae are present no premaxillae are known. We have insufficient information to decide if Saint-Seine's postrostral is a true postrostral (as it would be if the ethmoid commissure lay on the rostral), or if his lateral rostrals are toothless premaxillae ; depending on the interpretation of the snout bones the species could be derived from either the pholidophorid line or the ichthyokentemid line, or independently from the parasemionotids by fragmentation of a median rostro-premaxillary.

The Ligulellidae is another monotypic family containing *Ligulella sluysi* (Saint-Seine, 1955 : 103) from the freshwater Kimeridgian of the Congo. The species is poorly known, and the only bone which has been described in the snout is a massive, projecting rostral which bears teeth along both sides. Once again, the ethmoid commissure has not been seen, and no premaxillae are known. The species could be derived from the ichthyokentemid line by increase in size of the rostral, or from the pholidophorids by fusion and increase in size of the premaxillae.

To sum up this discussion of the relationships of the Pholidophoriformes, the order contained at least two lines, the pholidophorid and ichthyokentemid, differing in snout structure. The pholidophorid line could have evolved from the ichthyokentemids or could have arisen independently from the parasemionotids. The ichthyokentemids are more primitive than the pholidophorids and could not have evolved from them. The pholidophorid line gave rise to the Leptolepiformes, from which the teleosts are derived. The pleuropholids probably arose from the pholidophorid line. The archaeomaenids are similar to the pholidophorids in snout structure, but they exhibit two primitive characters which suggest that they may be an independent line from a parasemionotid-like ancestor. The majokiids and ligulellids are poorly known, but both could be derived either from the pholidophorids or the ichthyokentemids.

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VIII. LETTERING USED IN THE TEXT-FIGURES

ang.	angular
ao.	antorbital
a.p.cor.	anterior process of coracoid
apto.	autopterotic
aspo.	autosphenotic
b.h.c.	bucco-hypophysial canal
bo.	basioccipital
bpt.p.	basipterygoid process
br.	branchiostegal ray
bs.	basisphenoid
c.i.c.a.	canal for internal carotid artery
cl.	cleithrum
cor.	coronoid bone
d.ch.	distal ossification of ceratohyal
den.	dentary
d.f.	dilatator fossa
d.pcl.	dorsal postcleithrum
dpto.	dermopterotic
dspo.	dermosphenotic
ecp.	ectopterygoid
enp.	endopterygoid
epo.	epiotic
esc.	extrascapular
exo.	exoccipital
f.a.c.v.	foramen of anterior cerebral vein
f.d.n.	foramen of diazonal nerve
f.e.ps.a.	foramen of efferent pseudobranchial artery
f.f.	facial foramen
f.hm.	facet for articulation of hyomandibular
f.i.c.a.	foramen of internal carotid artery
f.ih.	facet for interhyal
f.l.e.	articular facet for lateral ethmoid on palatine
f.m.	foramen magnum
f.o.a.	groove for orbital artery
f.o.n.	foramen of occipital nerve
f.ot.n.	foramen of otic nerve
fr.	frontal
f.st.IX	foramen of supratemporal branch of glossopharyngeal nerve
f.vo.	articular facet for vomer on palatine
g.h.a.	groove for afferent pseudobranchial artery
gl.f.	glenoid facet
g.p.	gular plate
hm.	hyomandibular
ic.	intercalar
io.	infraorbital
iop.	interopercular
l.	lachrymal
l.e.	lateral ethmoid
M.b.	Meckelian bone
mcor.	mesocoracoid arch
mes.	mesethmoid
mpt.	metapterygoid
mx.	maxilla
mx.p.p.	maxillary process of palatine
myo.	myodome
na.	nasal
n.ap.	narial aperture
neu.	neural arch
omp.	oralo-mandibular pit-line
op.	opercular
op.p.	opercular process of hyomandibular
ors.	orbitosphenoid
pa.	parietal
pas.	parasphenoid
p.ch.	proximal ossification of ceratohyal
pf.	profundus foramen
pls.	pleurosphenoid
pmx.	premaxilla
pop.	preopercular
p.p.cor.	posterior process of coracoid
pro.	prootic
pro.b.	prootic bridge
p.t.f.	post-temporal fossa
q.	quadrate
ro.	rostral
sc.f.	scapular foramen
scl.	supracleithrum
smx.	supramaxilla
so.	supraorbital
soc.	supraoccipital
sop.	subopercular
ssc.	suprascapular
sub.	suborbital
sym.	symplectic
t.f.	trigeminal foramen
t.p.	transverse process
vo.	vomer
v.pcl.	ventral postcleithrum
I	foramen of olfactory nerve
II	optic fenestra
III	notch for oculomotor nerve
V mand.	canal for division of mandibular branch of trigeminal nerve
VI	foramen of abducens nerve
VII hm.	foramen for hyomandibular trunk of facial nerve
VII lat.	foramen for lateralis branches of facial nerve
VII p.	course of palatine nerve
IX	glossopharyngeal foramen
X	vagus foramen

PLATE 1

Ichthyokentema purbeckensis (Davies)

FIG. 1. Complete fish. P. 8378. × 1.8.
FIG. 2. Head showing medial surface of cheek bones of the right side. P. 1073. × 4.5.

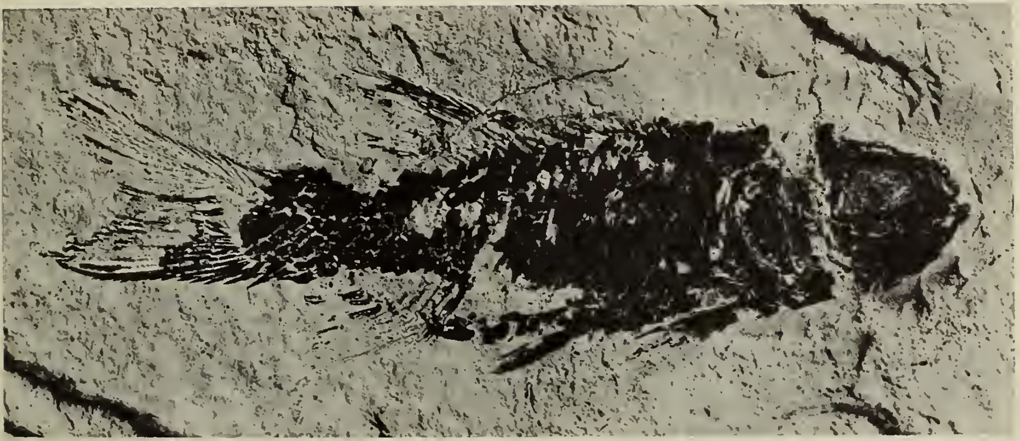

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PLATE 2

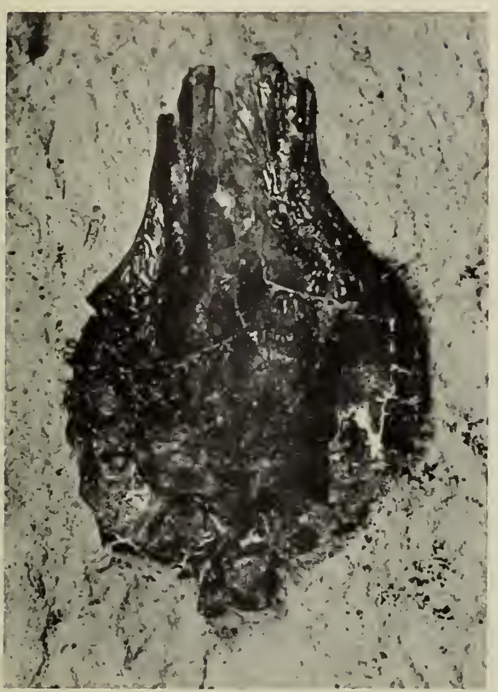
Ichthyokentema purbeckensis (Davies)

FIG. 3. Skull lacking ethmoid region in dorsal view. P. 44949. × 5.5.

FIG. 4. Anterior end of neurocranium in dorsal view, to show rostral. P. 44927. × 15.

FIG. 5. Snout region in lateral view, to show the nasal (na.), rostral (ro.) and premaxilla (pmx.). P. 8379. × 8.5.

FIG. 6. Photomicrograph of flank scale in optical section, to show bone cell spaces and canals of Williamson (c.W.). P. 45031. × 360.



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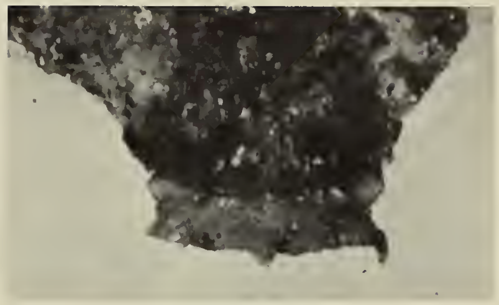

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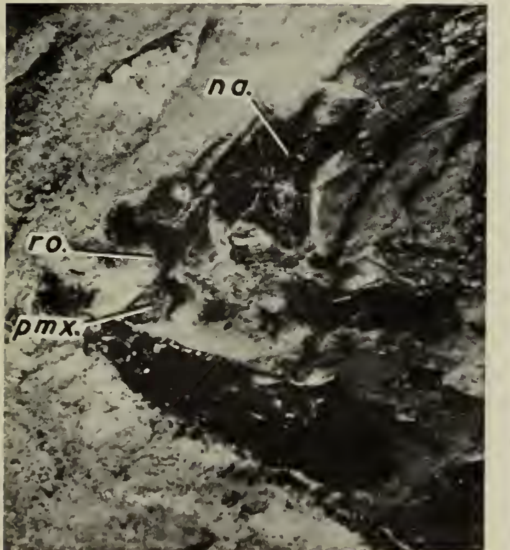

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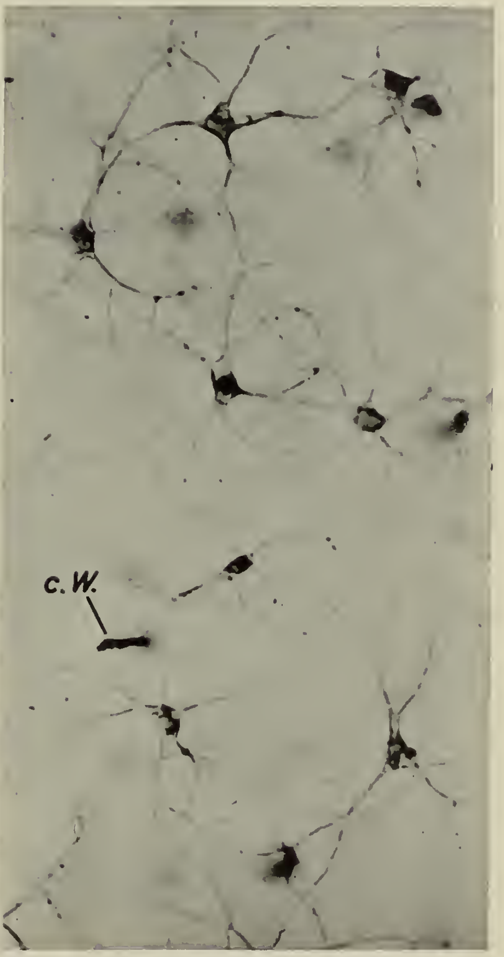

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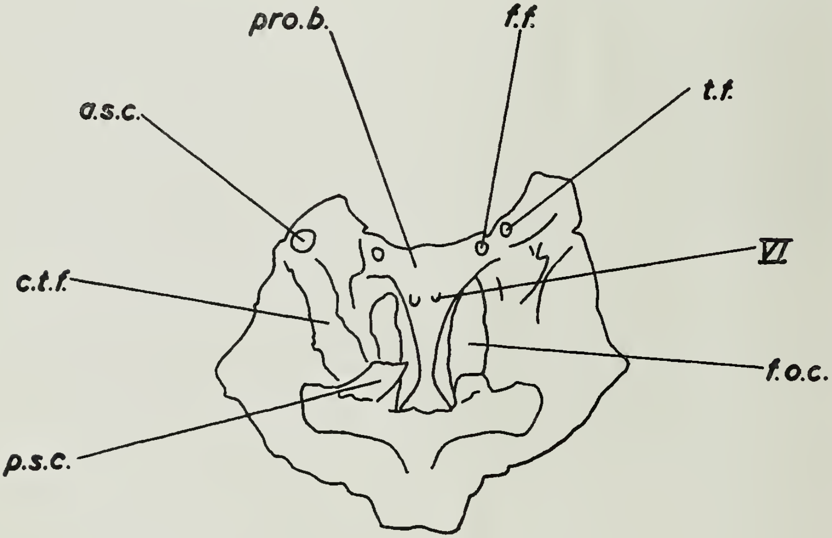
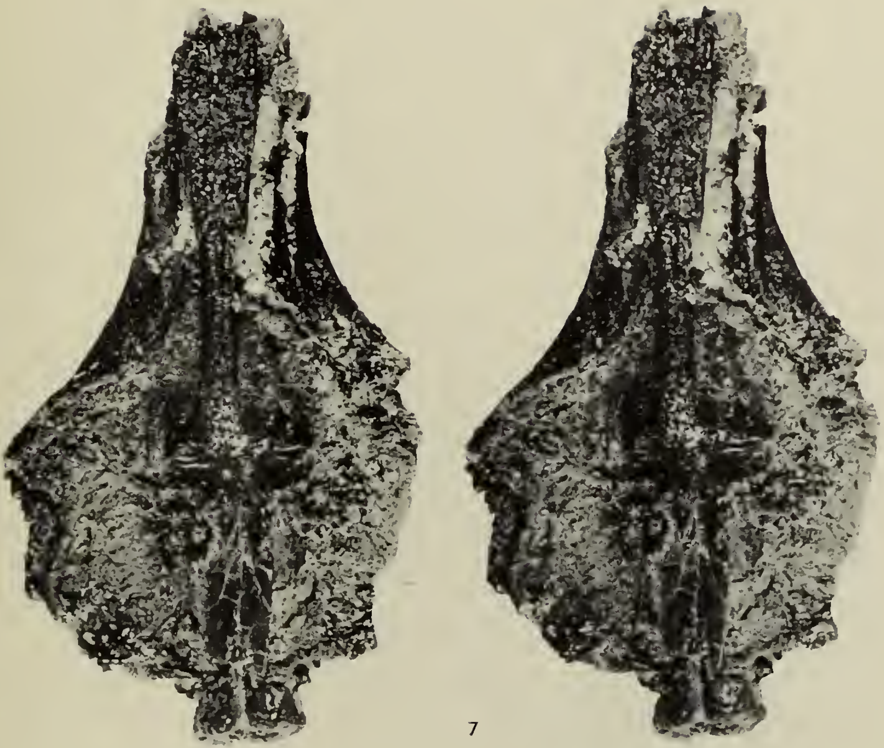
PLATE 3

Ichthyokentema purbeckensis (Davies)

FIG. 7. Stereoscopic pair of neurocranium in ventral view. P. 44929. × 6.5.

FIG. 8. Stereoscopic pair of incomplete neurocranium in dorsal view, to show the cranial cavity : a.s.c. ; anterior semicircular canal in prootic : c.t.f. ; space, filled in life by cartilage, in the floor of the post-temporal fossa : f.f. ; facial foramen : f.o.c. ; fenestra between the cranial cavity and the otolith chamber : pro.b. ; prootic bridge : p.s.c. ; posterior semicircular canal in epiotic : t.f. ; trigeminal foramen : VI ; abducens foramen. P. 44934. × 8.





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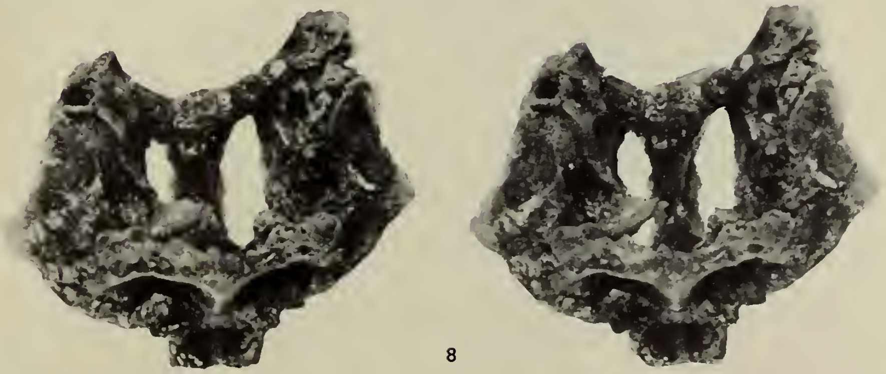

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PLATE 4

Ichthyokentema purbeckensis (Davies)

FIG. 9. Stereoscopic pair of mandible of the right side in medial view. P. 44974. × 9.5.

FIG. 10. Stereoscopic pair of endoskeletal pectoral girdle and incomplete cleithrum of the right side in medial view. P. 44967. × 9.5.

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